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The systematics of the scorpion subfamily Uroctoninae (Scorpiones: Chactidae)

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ARTÍCULO:

THE SYSTEMATICS OF THE SCORPION SUBFAMILY UROCTONINAE (SCORPIONES: CHACTIDAE)

Michael E. Soleglad & Victor Fet

Abstract:
The systematics of scorpion subfamily Uroctoninae (Scorpiones: Chactidae) is described and illustrated in detail. Diagnoses of both genera, *Uroctonus* and *Anuroctonus*, and all species and subspecies are provided including an illustrated key and distribution map. For genus *Anuroctonus*, a comprehensive set of collections was examined, covering its entire geographical range in the USA (California, Nevada, Utah, Idaho) and Mexico (Baja California Norte). A new species, *Anuroctonus pococki* sp. nov. and its subspecies, *A. pococki bajae* ssp. nov., distributed in southern coastal California and Baja California Norte, Mexico, are described. It is established that the type species, *A. phaiodactylus*, is restricted to the Great Basin area of the United States, located in south-eastern California, Nevada, Utah, and Idaho.
Key words: Scorpiones, Chactidae, Uroctoninae, *Uroctonus, Anuroctonus*, systematics.
Taxonomy: *Anuroctonus pococki*, **sp. n.**; *Anuroctonus pococki bajae*, **ssp. n.**

Sistemática de la subfamilia Uroctoninae (Scorpiones: Chactidae)

Resumen: Se describe e ilustra en detalle la sistemática de la subfamilia Uroctoninae (Scorpiones: Chactidae). Se aportan diagnosis de los dos géneros, *Uroctonus* y *Anuroctonus*, y de todas sus especies y subespecies, incluyéndose clave ilustrada y mapa de distribución. En el caso del género *Anuroctonus* se examinó una amplia serie de colecciones, cubriéndose toda su área de distribución en Estados Unidos (California, Nevada, Utah, Idaho) y Méjico (Baja California Norte). Se describen una nueva especie, *Anuroctonus pococki* sp. nov., y su subespecie, *A. pococki bajae* ssp. nov., cuya área cubre las zonas costeras meridionales de California y Baja California Norte, Méjico. Se establece que la especie tipo, *A. phaiodactylus*, está restringida a la zona de la Great Basin, en Estados Unidos, que incluye el sureste de California, Nevada, Utah, y Idaho.
Palabras clave: Scorpiones, Chactidae, Uroctoninae, *Uroctonus, Anuroctonus*, sistemática.
Taxonomy: *Anuroctonus pococki*, **sp. n.**; *Anuroctonus pococki bajae*, **ssp. n.**

Introduction

Recently, Soleglad & Fet (2003b: 94–105), in their analysis of high-level systematics of extant scorpions, presented a phylogenetic revision of the chactoid family Chactidae. In this revision, three subfamilies were defined, Chactinae, Brotheinae, and Uroctoninae. Subfamily Chactinae was further divided into two tribes, Chactini (composed of South American genera *Chactas*, *Teuthraustes*, and *Vachoniochactas*) and Nullibrotheini (composed of North American genus *Nullibrotheas*). Subfamily Brotheinae was also divided into two tribes, Brotheini (composed of South American genera *Brotheas*, *Broteochactas*, and *Hadrurochactas*, placed in subtribe Brotheina, and genus *Neochactas*, placed in subtribe Neochactina) and Belisariini, composed of European genus *Belisarius*. Subfamily Uroctoninae, the subject of the current paper, was defined as composed of two North American genera, *Uroctonus* and *Anuroctonus*. In their revision, Soleglad & Fet (2003b: 95) provided a key to the subfamilies, tribes, and subtribes of family Chactidae.

In this contribution, we discuss in detail the systematics of the newly defined chactid subfamily Uroctoninae. A detailed set of diagnostic characters for Uroctoninae is provided that enhances the original set of synapomorphies presented in the revision of Soleglad & Fet (2003b). Two uroctonine genera, *Uroctonus* and *Anuroctonus*, are contrasted in detail providing new differentiating characters in their diagnoses. In addition, a detailed revision of the genus *Anuroctonus* is given, including the description of a new species and subspecies. This analysis was based on the study of over 450 *Anuroctonus* specimens from a comprehensive set of diverse localities spanning the entire range of the genus. All important collections were studied, including but not limited to, California Academy of Sciences (CAS), which houses the vast Stanley C. Williams and Richard Haradon collections; the Bean Museum (Brigham Young University, Utah), which includes the Donald Allred collection; the United States National Museum (USNM), which includes the type specimen and the collection of Scott Stockwell; and the private collections of Robert Anderson (Idaho State University) and Graeme Lowe. Specimens from the most northern recorded locality (Idaho) and the most southern locality (El Progreso, Baja California Norte), were examined. An illustrated key and distribution map is provided for all genera, species, and subspecies assigned to subfamily Uroctoninae.

Subfamily Uroctoninae is composed of two ecologically divergent North American genera, *Anuroctonus* and *Uroctonus*. *Anuroctonus* is a desert burrowing scorpion (Williams, 1966) found in California, Nevada, Utah, and Idaho (USA), and in Baja California Norte, Mexico. *Uroctonus* is a less xeric genus, found in western states of USA, California and Oregon, from sea coast to 2400 m in the montane forests (Gertsch & Soleglad, 1972; Hjelle, 1972; Williams, 1986). *Uroctonus* and *Anuroctonus* are essentially allopatric in coastal California, *Anuroctonus* replacing *Uroctonus* south of the Monterey Peninsula (Hjelle, 1972), extending south into Baja California and east into the Great Basin. In central-eastern California, their ranges overlap somewhat, especially in Kern, Los Angeles, and Inyo counties. Distribution of *Anuroctonus* and *Uroctonus* is shown in the map (Fig. 31).

Williams (1966), in his study on the burrowing habits of *Anuroctonus*, excavated and measured 25 burrows in San Diego County, California. There burrows, all similar in construction, were quite extensive, measuring anywhere from 18 to 42 cm in depth. Females were found in 21 of these burrows, which were always considerably longer than the those of the males (deepest only 19 cm). While collecting *Anuroctonus* in the Anza-Borrego Desert State Park at night using UV detection, M. S. found small clusters of burrows, with just small portions of the animal protruding from each burrow entrance, presumably the extreme carapace edge and/or pedipalp fingers—barely recognizable as a scorpion. Only the adult male was encountered out of the burrow and would stand its ground while being collected, never attempting to escape or run into a burrow. Presumably immatures and females were in the burrow entrances and, in stark contrast to the male, were incredibly skittish; all would disappear, in unison, at the slightest disturbance. In support of this observation, the number of male specimens examined in this study far exceeds that of females, in a ratio of 3.3 to 1.2.

Methods and Material

SEM microscopy

Scorpion structures were removed from the animals and fixed for 12 hours in 0.1 M sodium cacodylate with 2.5 % gluteraldehyde (freshly prepared). After rinse/soak for 12 hours in plain 0.1 M sodium cacodylate, specimens were post-fixed for 2 hours in freshly prepared 1 % osmium tetroxide again in sodium cacodylate. Specimens were rinsed three times with distilled water and dehydrated in an ethanol series (50, 75, 95, and two changes of 100 %) before being dried and coated with gold/palladium (ca. 10 nm thickness) in a Hummer sputter coater. Digital SEM images were acquired with a JEOL JSM-5310LV at Marshall University, West Virginia. Acceleration voltage (10–20 kV), spot size, and working distance were adjusted as necessary to optimize resolution, adjust depth of field, and to minimize charging.

Terminology and conventions

All measurements (i.e., morphometrics) presented in this paper are in millimeters (*mm*). For meristic and morphometric statistical data presented in this paper the following conventions are used:

min–max* (*mean*) (±*SD*) [*n*]:{*cmin–cmax*} → *cv

for the above *statistical data group*, *min* = minimum value, *max* = maximum value, *SD* = standard deviation, *n* = number of samples, *cmin* = corrected minimum (*mean-SD*), *cmax* = corrected maximum (*mean+SD*), *cv* = coefficient of variability (*SD/mean*). The range established by the corrected minimum and maximum is referred to as the *plus-minus standard error* range. Each statistical data group represents a dataset based on some specified partitioning (e.g., a species, a subspecies, a population, a genus, a gender, etc.). Specific techniques used in the analysis of morphometric ratios presented in this paper are described in detail in Fet & Soleglad (2002). In addition to establishing plus-minus standard error ranges, the statistical data group was subjected to variance analysis to further quantify the *statistical differences* between two groups.

Terminology describing chelal finger dentition and pedipalp chelal ornamentation follows that described and illustrated in Soleglad & Sissom (2001); sternum terminology follows that described and illustrated in Soleglad & Fet (2003a); and terminology of the pedipalp patella and metasomal carinae, and classification of neobothriotaxy types follows that described in Soleglad & Fet (2003b).

Cladistic Analysis Software

Software package PAUP* Version 4 (beta) (Swofford, 1998) was used for Maximum Parsimony (MP) analysis of morphology based character codings.

Abbreviations

List of depositories: AMNH, American Museum of Natural History, New York, New York, USA; BEAN, Bean Museum, Brigham Young University, Provo, Utah, USA; BH, Personal collection of Blaine Hébert, Los Angeles, California, USA; CAS, California Academy of Sciences, San Francisco, California, USA; CAS-S, Stahnke collection, California Academy of Sciences, San Francisco, California, USA; GL, Personal collection of Graeme Lowe, Philadelphia, Pennsylvania, USA; JB, Personal collection of Joe Bigelow, Yuma, Arizona, USA; JVZ, Personal collection of J. Van Zee, Los Angeles, California, USA; MES, Personal collection of Michael E. Soleglad, Borrego Springs, California, USA; NRS, Naturhistoriska Riksmuseet, Stockholm, Sweden; RA, Personal collection of Robert Anderson, Idaho State University, Pocatello, Idaho, USA; UCR, University of California Riverside, Riverside, California, USA; USNM, United States National Museum (Smithsonian Institution), Washington, DC, USA; and WDS, Personal collection of W. David Sissom, Canyon, Texas, USA.

Other: [??] signifies questionable locality; ABDSP, Anza-Borrego Desert State Park, San Diego and Riverside Counties, California, USA.

Systematics

ORDER SCORPIONES C. L. Koch, 1850

SUBORDER NEOSCORPIONES Thorell & Lindström, 1885

Infraorder Orthosterni Pocock, 1911

Parvorder Iurida Soleglad & Fet, 2003

Superfamily Chactoidea Pocock, 1893

Family Chactidae Pocock, 1893

Subfamily Uroctoninae Mello-Leitão, 1934

Uroctoninae can be defined by the following set of derived and primitive characters (after Soleglad & Fet, 2003b: 80–82). **Synapomorphies:** distance between patellar trichobothria esb_1 and esb_2 is considerably greater than the distance between em_1 and em_2; ventral edge of cheliceral movable finger with dentition; ventroexternal carina (*V1*) of chela curves inward distally towards internal condyle of movable finger; patellar spurs DPS and/or VPS well-developed; stigmata medium to long in size, oval in shape; lateral eyes number 3–4. **Important Symplesiomorphies:** <u>derivations originating from clade (Superstitioniidae + (Euscorpiidae + Chactidae)):</u> chelal trichobothrium *ib* situated at the extreme base of the fixed finger or palm; chelal trichobothrial series V_1-V_4 is shortened, with V_1-V_2-V_3 juncture usually angling towards the internal aspect of the palm; <u>derivations originating from clade (Euscorpiidae + Chactidae):</u> chelal trichobothrium *it* positioned on palm; chelal finger trichobothrium *eb* closest to the finger edge, *esb* angling towards the dorsal edge; patellar trichobothrium v_3 just proximal of, or at the midpoint of segment, and definitely proximal of trichobothria *est* and et_3; <u>derivations originating from clade (Chactidae):</u> femoral trichobothrium *d* positioned equal or distal to *i*; chelal trichobothrium Eb_1 situated on ventral surface or on *V1* carina; genital operculum of female separated for most of its length. Uroctoninae is separated from its two sister subfamilies by its synapomorphies as well as other derived characters for these subfamilies, such as major fixed neobothriotaxy Type *Ch1* in Chactinae and the loss of the ventral median spinule row of the leg tarsus in Brotheinae.

Both uroctonine genera have been previously associated with the North American scorpion family Vaejovidae. Before Soleglad & Fet's (2003b) revision, *Uroctonus* had long been included in the Vaejovidae. *Anuroctonus* was also included in the Vaejovidae, or declared *incertae sedis* (Francke & Soleglad, 1981); Stockwell (1989, 1992) associated *Anuroctonus* with the Iuridae, following Stahnke (1974). In addition to the stated derived characters, these two chactid genera also lack several characters that are common to most vaejovids: ventral patella trichobothrium v_3 is not located on the distal external aspect of the segment as in the vaejovids, but is found on the ventral surface more mid-segment in position; the genital operculum sclerites of the female are not connected by a membrane as in the vaejovids, but are separated for most of their length; the termini of the dorsal lateral carinae of metasomal segment IV are not flared as in the vaejovids (genera *Paruroctonus* and *Smeringurus* are an exception), but instead, coincide with the articulation mechanism; the Dorsal Patellar Spur carina (DPS_c) is not developed as in the Vaejovidae, being absent; the base of the lamina of the hemispermatophore does not exhibit a lamellar hook as seen in most vaejovids; the ventral median carina of metasomal segment V does not terminate into a single carina but instead bifurcates distally into a Y-shaped formation.

Major characters used to differentiate the genera, species, and subspecies of the subfamily Uroctoninae include the pedipalp trichobothrial patterns, dentition of the chelicerae, dentition of the chelal fingers, granulation of the carapace, and morphometrics involving the metasoma. Note that the meristic and continuous data ranges and means stated in the key are based on the plus-minus standard error ranges established elsewhere in this paper.

Illustrated key to genera, species, and subspecies of subfamily Uroctoninae

1. Neobothriotaxy type *Ch3* present on pedipalp (Figs. 29–30); ventral edge of cheliceral movable finger with minimal crenulation, one to four small closely grouped denticles situated on proximal half; serrulae absent on ventral edge of cheliceral movable finger (Figs. 2 and 11); chelal movable finger equipped with six internal denticles (ID) (Fig. 5); pedipalp patella with a well developed *single* Dorsal Patellar Spur (DPS), the Ventral Patellar Spur (VPS) vestigial (Fig. 13); ventral carinae of sternite V and metasomal segments I–III noticeably raised from surface, broadly crenulate, and taper conspicuously in an anterior to posterior direction, on segment IV carinae smooth to obsolete (Fig. 15); carapace anterior edge with modest indentation (Figs. 7–8, 38–42); telson aculeus of sexually mature males swollen at its base (Fig. 20) ….. (genus ***Anuroctonus***) **2**

– Orthobothriotaxy present on pedipalp (Fig. 28); ventral edge of cheliceral movable finger with significant crenulation, four to seven denticles situated throughout finger edge; serrulae present on ventral edge of cheliceral movable finger (Fig. 1); chelal movable finger equipped with 8–9 internal denticles (ID) (Figs. 3–4); pedipalp patella with a well-developed *double* DPS and a VPS (Fig. 12); ventral carinae of sternite V and metasomal segments I–IV weak to well granulated, oriented essentially parallel on segments II–IV (Fig. 14); carapace anterior edge with conspicuous indentation (Fig. 6); telson aculeus of sexually mature males not swollen at its base (Fig. 18) ……………………… (genus ***Uroctonus***) …. **4**

2. Ventral trichobothria of pedipalp chela number 16–20 (18) (Fig. 49); interocular area of carapace of male granulated (Figs. 8, 38–40); chelal digital (*D1*) carina well-developed (Fig. 47); metasomal segment V ratio (L/W) of 2.95–3.25 (3.10) for male (Fig. 52) ……………………….. (***A. pococki*, sp. nov.**) …. **3**

– Ventral trichobothria of pedipalp chela number 13–15 (14) (Fig. 49); interocular area of carapace of male smooth, or with minor granulation on extreme distal edge (Figs. 7, 41–42); chelal digital (*D1*) carina obsolete to weakly developed (Fig. 48); metasomal segment V ratio (L/W) 2.75–2.96 (2.85) for male (Fig. 52) …………………..... ***A. phaiodactylus***

3. Ventral trichobothria of pedipalp chela number 17–21 (19) (Fig. 49); chelal ventroexternal (*V1*) carina generally smooth (Fig. 43); chelal digital (*D1*) carina usually darkly pigmented (Fig. 29) …. ***A. p. pococki***

– Ventral trichobothria of pedipalp chela number 16–18 (17) (Fig. 49); chelal ventroexternal (*V1*) carina pitted to distinctly granulated (Figs. 44–45); chelal digital (*D1*) carina pigmentation absent or faintly present (Fig. 30) ………..…. ***A. p. bajae*, ssp. nov.**

4. Ventral carinae of metasomal segments II–IV distinctly granulated; carapace granular on lateral areas; median eyes small but not noticeably reduced; overall color dark mahogany, or if lighter yellow, pedipalpal and metasomal carinae conspicuously contrasted with darker color (Figs. 32–33) ………. …. **5**

– Ventral carinae of metasomal segments II–IV essentially obsolete; carapace generally smooth on entire surface; median eyes are noticeably reduced; overall color yellow to golden brown with little contrasting markings ………. ***U. grahami*** (troglobytic species)

5. Setal formula of dorsal lateral carinae for metasomal segments I–IV is 1-2-2-2; length/width ratio of metasomal segments III–IV with median value 1.382/1.741 and 1.336/1.678, in male and female, respectively (see Table I) …….. (***U. mordax***) …. **6**

– Setal formula of dorsal lateral carinae for metasomal segments I–IV is 1-1-1-2; length/width ratio of metasomal segments III–IV with median value 1.679/2.200 and 1.474/1.853, in male and female, respectively (see Table I) ……………. ***U. franckei***

6. Fixed and movable fingers of chelae with seven and eight internal denticles (ID), respectively (Fig. 3)….. …………………..………….…..…… ***U. m. mordax***

– Fixed and movable fingers of chelae with eight and nine internal denticles (ID), respectively (Fig. 4) ……………………………….……... ***U. m. pluridens***

Comparison of Genera

We now contrast the genera *Uroctonus* and *Anuroctonus*. Figures 1–30 illustrate important structures common to, as well as distinguishing, these two genera.

Chelicerae (Figs. 1–2, 11): Genera *Uroctonus* and *Anuroctonus* have in common the crenulated ventral edge of the cheliceral movable finger, a derived character for subfamily Uroctoninae. However, the degree of this crenulation is quite different in the two genera. In *Uroctonus* (Fig. 1), we see that the crenulation is quite substantial, providing good-sized pigmented denticles for most of the finger's ventral edge. In contrast, we see in *Anuroctonus* (Fig. 2) quite limited dentition on the basal half of the edge, numbering anywhere from one to four small denticles (two being typical), the basal denticle the largest. Hjelle (1972: Fig. 36) reported anywhere from one to seven denticles on this edge for *Uroctonus*, with an average, depending on the population, of 2.0–4.3. The cheliceral fingers are more elongated on *Anuroctonus*, the differences in lengths of the distal denticles of the movable finger are considerable, the ventral denticle considerably longer than its dorsal counterpart. In *Uroctonus*, the ventral distal denticle is longer as well, but not as exaggerated as seen in *Anuroctonus*. These differences are quite apparent when comparing their external views as shown in Figs. 1–2.

Curiously, *Uroctonus* exhibits serrulae on the distal aspect of the ventral edge of the movable finger while it is absent in *Anuroctonus*. Of particular interest, we see that *Anuroctonus* has a large setal brush on its ventral edge (Fig. 11), the distal portion aligned in a precise curved line conforming to the curve of the distal tine. On the extreme distal aspect we can see a small raised ridge from which a single row of setae originate. This row of setae corresponds in location to the serrula found in *Uroctonus*. The presence of serrula (likely an adaptive grooming device) in Recent scorpions is quite curious at best due to its apparent "randomness" of occurrence, providing no real consistency within phylogenetic lineages. For example, we find serrula in the primitive scorpion genus *Pseudochactas* (family Pseudochactidae; Soleglad & Fet, 2003b: Fig. 49), but it is missing from the buthoids and the chaeriloids; it is present in the Old World iuroids (family Iuridae, genera *Calchas* and *Iurus*), but absent in the New World iuroids (family Caraboctonidae, subfamilies Caraboctoninae and Hadrurinae); it is present in genus *Chactopsis* (Soleglad & Sissom, 2001: Fig. 140), but absent in the other ten euscorpiid genera; it is present in most vaejovids but absent in related genera *Paruroctonus*, *Smeringurus*, and *Vejovoidus*; and it is not reported for any of the scorpionoids. We (Fet et al., in progress) are examining the microstructure of serrula in all Recent scorpion groups using SEM micrography, attempting to determine if this curious structure can be analyzed for further diagnostic purposes. In addition, we are also investigating those related scorpion groups that lack serrula but do possess significant setal brushes as that illustrated here for *Anuroctonus* (Fig. 11), under the assumption that these structures may be functionally homologous.

Chelal finger dentition (Figs. 3–5): As seen in most chactoids (the superstitioniids are an exception) the median denticle (MD) row in these genera is oriented in a straight line. Both of these genera possess outer denticles (OD) positioned in the MD row, and adjacent inner denticles (ID) situated on the inner edge of the finger. Both genera also exhibit an enlarged denticle on the extreme base of the movable finger edge: in *Uroctonus* it is definitely an inner denticle ID, while in *Anuroctonus*, it is indeterminable since the denticle is situated in the median row. Diagnostic between the two genera is the number of inner denticles (ID) found on the movable finger edge. In *Anuroctonus* (Fig. 5) we see only six ID denticles, one is absent from the adjacent sixth OD denticle. In *Uroctonus*, the number of ID denticles is variable, depending on the subspecies, eight in *U. m. mordax* (Fig. 3) and other species, and nine for *U. m. pluridens* (Fig. 4). In the latter, we also see an additional denticle group (DG), seven; in *U. m. mordax* and *Anuroctonus*, we have six DGs.

Carapace (Figs. 6–7, 8): Both genera exhibit an indentation on the anterior edge of the carapace, accompanied by a subtle median furrow extending to the distal aspect of the median eyes. In *Uroctonus* (Fig. 6), this indentation is quite deep and well-defined, whereas in *Anuroctonus* (Figs. 7–8) the indentation is shallow and more subdued. Both genera have more than two lateral eyes on each side of the carapace, which is considered a derivation for Uroctoninae from the typical two eyes found in most chactids. In both genera, the most anterior eye is the largest and the most posterior the smallest, a typical configuration found in scorpions with three lateral eyes. Interestingly, as first reported by Gertsch & Soleglad (1972: Fig. 23), *Anuroctonus* has a small *fourth* eye, situated above eyes 2 and 3 (Fig. 10). González-Sponga (1973) also reported brotheine *Brotheas mingueti* with four eyes.

Pedipalp patellar carinae and spurs (Figs. 12–13): As all chactids, *Uroctonus* and *Anuroctonus* exhibit the typical five-carinae configuration for the pedipalp patella, as defined by Soleglad & Fet (2003b: 52–58): two dorsal carinae, DE_c and DI_c, two ventral, VE_c and VI_c, and one external, EM_c, which is essentially vestigial in these genera. Although both genera display at least one well-developed patellar spur, neither the DPS_c or VPS_c carinae are present. For example, in contrast, the DPS_c is present in all vaejovids, considered a synapomorphy for the family. Diagnostic for *Uroctonus* and *Anuroctonus* is the development of the patellar spurs. In *Uroctonus* we find well developed DPS and VPS, both forming *double* spurs (Fig. 12). In *Anuroctonus*, the DPS is well developed but single in structure, and the VPS is vestigial, essentially obsolete (Fig. 13). The presence of these patellar spurs is a synapomorphy for subfamily Uroctoninae, as they are essentially vestigial or obsolete in the other two subfamilies, Chactinae and Broteinae.

Mesosoma, metasoma and telson (Figs. 14–21): The stigmata of *Uroctonus* and *Anuroctonus* are of average size, somewhat elongate, and sub-oval in shape (Figs. 14–15). This is considered a derivation from the typical small circular stigma found in the other chactids. Except for *Brotheas*, which has large slit-like stigmata, the other chactids have small sub-oval to circular stigmata.

Diagnostic of the chactids, both *Uroctonus* and *Anuroctonus* have their dorsal lateral carinae terminus of metasomal segment IV coinciding with the articulation condyle of this segment, lacking any indication of a flared terminus commonly exhibited in the vaejovids. Also common to both of these genera is the Y-shaped bifurcated terminus of the ventral median carina of metasomal segment V (Figs. 14–15). Williams and Savary (1991: Fig. 8) reported this character for *Uroctonus*, using it as a distinguishing character to separate, in part, *Uroctonus* from their new genus *Uroctonites*, a vaejovid. Although the metasoma of *Uroctonus* and *Anuroctonus* share chactid characteristics, they are also quite distinct within the two genera. In *Anuroctonus* we see a very peculiar and unique development of the ventral lateral and ventral median carinae of segments I–III (and also true for the carinae on sternite V), highly raised above the segment surface, providing an exaggerated rounded crenulate appearance. In addition, these carinae also taper considerably from an anterior to posterior direction. In *Uroctonus*, the carinae are weakly to medium granulated, not exhibiting the raised crenulate appearance as seen in *Anuroctonus*; and, except for segment I, the carinae are somewhat parallel in their orientation, not tapering. Laterally, on metasomal segment V, we see that in *Anuroctonus* the dorsal lateral carinae flare distal towards the telson (Fig. 17); in *Uroctonus*, the terminus of segment V is more rounded, the dorsal lateral carinae not flaring towards the telson (Fig. 16). We suspect that this flaring may be the cause, in part, of the missing "vesicular tabs" in *Anuroctonus*, occurring in both male and female (Figs. 20–21). Typically for Recent scorpions, the dorsal base of the telson vesicle is equipped with lateral projections of the cuticle, referred to here as "tabs". These are present in both genders of *Uroctonus* (Figs. 18–19). Possibly the flared aspect of metasomal segment V may interfere spatially with these "tabs". The telson of sexually mature males of *Anuroctonus* species is quite unique in its own right—with its highly swollen rectangular shape vesicle (similar to that seen in many species of *Euscorpius* (family Euscorpiidae)), and the swollen base of the aculeus, unprecedented in Recent scorpions (Fig. 20). Sexual dimorphism is also apparent in genus *Uroctonus*, where the vesicle of the mature male is more swollen and the vesicle-aculeus juncture very distinct (Figs. 18–19).

Sternum, genital operculum, and pectines (Figs. 22–25): Both genera exhibit well-defined Type 2 sterna (Soleglad & Fet, 2003a), with well-formed convexed lateral lobes and somewhat deep apical depressions (Figs. 22–25). In *Anuroctonus*, the sternum is slightly wider than long whereas in *Uroctonus*, it is definitely wider than long. In both genera, the sclerites of the genital operculum of the female are essentially separated along their entire length, characteristic of the chactids. In addition, the inner proximal edges of the plates of the female genital operculum are more rounded than those seen in the male (Figs. 23 and 25). In males, the genital papillae of *Uroctonus* extends beyond the posterior edge of the genital operculum (Fig. 22), whereas in *Anuroc-*

tonus, the proximal extremities of the papillae are not as pointed and usually are covered by the genital operculum (Fig. 24).

Both genera have a reduced number of pectinal teeth in proportion to their maximum size, typical of the non-vaejovid chactoids (i.e., the pectinal tooth counts are relatively larger in family Vaejovidae (Soleglad & Fet, 2003b: 61–65)). This reduction is more apparent in *Anuroctonus* whose pectinal tooth counts range 6–12 in male, and 4–9 in female (see histogram in Fig. 37). In *Uroctonus*, we see higher ranges in tooth counts, 11–15 in male, and 8–12 in female (Hjelle, 1972: 18). The middle lamellae are considerably more numerous in *Uroctonus*, those following the more rectangular shaped basal lamellar plate being round "bead-like" in shape (Figs. 22–23). In *Anuroctonus*, the middle lamellae are reduced, with a large rectangular basal plate occupying most of the area (Figs. 24–25). In both genera, the sensory areas are much more developed in males than in females; in the latter, sensory areas are limited to the distal inner edges of the tooth.

Hemispermatophore (Figs. 26–27): The hemispermatophores in both genera are quite similar in their overall shape, proportions, and structure. The hemispermatophore is lamelliform (as in all scorpions of parvorder Iurida); a well-defined truncal flexure is present separating the trunk from the lamina; the lamina is long and thin, exhibiting a conspicuous basal constriction above the well developed dorsal trough and simple capsular area. The lamina is lacking a basal hook. The capsular area is simplistic exhibiting a moderately sclerotized structure: on the dorsal aspect this structure curves upwards slightly forming a somewhat wide blunt hook-like process. This process is a little more substantial in *Uroctonus*. The lamina in *Uroctonus* is a little wider at its base (Fig. 26) than *Anuroctonus*, in which the base tapers into a somewhat thin terminus (Fig. 27). The hemispermatophores of these genera share the same simplistic capsular area as its two sister subfamilies, Chactinae and Brotheinae; however, in both latter subfamilies the lamina is long, thin, and very tenuous in shape.

Chelal carinae (Figs. 28–30, 43–48): The overall chelae carinal structure is the same in *Uroctonus* and *Anuroctonus*, both complying with the "10-carinae" configuration (see Soleglad & Sissom, 2001: 41–44). Common to both genera is the strong ventroexternal (*V1*) carina whose terminus curves conspicuously towards the internal aspect of the palm, terminating between trichobothria Et_1 and V_1 (Figs. 28–30), this is considered a synapomorphy for the subfamily Uroctoninae. The dorsosecondary (*D3*) and ventromedian (*V2*) carinae are quite weak in these genera, giving the palm an overall flat look. In genus *Anuroctonus*, the relative development of the digital (*D1*) and *V1* carinae are diagnostic for the species and subspecies defined in this paper (Figs. 43–48).

Leg tarsus armature: The leg tarsus armature of *Uroctonus* and *Anuroctonus* conform to configuration 5 as defined by Soleglad & Fet (2003b: 27–28: Figs. 34, 39): paired ventral lateral rows of small to medium setae with small sockets are accompanied by a median row of spinules. The lateral setal pairs are reduced in these genera, the setae are somewhat thin, and the median ventral spinule row of stout spinules terminates distally with a single pair of spinules. Except for subfamily Brotheinae, where the median ventral spinule row is absent, other chactids conform to this configuration. In subfamily Chactinae, the lateral setal pairs are more substantially developed, especially in tribe Chactini.

Trichobothrial patterns (Figs. 28–30): *Uroctonus* and *Anuroctonus* exhibit classic chactid and euscorpiid, in part, trichobothrial characteristics: the chelal finger internal trichobothrial series *ib-it* is situated on the palm, well below the fixed finger; chelal finger trichobothria *est-esb-eb* juncture angles toward the dorsal aspect of the fixed finger, *eb* situated quite close to the articular membrane of the movable finger; the chelal ventral trichobothria series V_1-V_4 is somewhat short, the V_1-V_2-V_3 juncture usually angles toward the internal aspect of the palm; patellar trichobothrium v_3 is located more midsegment on the ventral surface of the segment. See Soleglad & Sissom (2001: 45–55: Figs. 73–118) and Soleglad & Fet (2003b: 36–52, 98–100: Figs. 66–90, 118–125), for the complete description and illustrations of the trichobothrial patterns of superfamily Chactoidea (families Chactidae, Euscorpiidae, Superstitioniidae, and Vaejovidae).

Anuroctonus can be distinguished from *Uroctonus* by the major variable neobothriotaxy occurring on the ventral surface of the chela and ventral and external aspects of the patella. Soleglad & Fet (2003b: 50) classified this neobothriotaxy derivation as *Ch3*, contrasting it from other neobothriotaxic derivations seen in the subfamilies Chactinae (*Ch1*) and Brotheinae (tribe Brotheini) (*Ch2*). *Ch3* neobothriotaxy is variable and unique to genus *Anuroctonus* (Figs. 29–30). The variation occurs in the number of accessory trichobothria found on the chela and patella. In particular, the number of ventral accessory trichobothria found on the chela exhibits considerable variation providing an excellent diagnostic character for differentiating the species of *Anuroctonus* described in this paper (discussed in detail below). Genus *Uroctonus* is orthobothriotaxic (Fig. 28) and therefore provides an important reference point for establishing homologous trichobothria in those genera whose patterns are obscured by major neobothriotaxy. The brotheine genus *Belisarius* is also orthobothriotaxic and, as *Uroctonus*, provides this important function as well. In fact, the trichobothrial patterns of *Uroctonus* and *Belisarius* are strikingly similar, both illustrating the classic chactid pattern not obscured by neobothriotaxy (Soleglad & Fet, 2003b).

Genus *Uroctonus* Thorell, 1876

Uroctonus Thorell, 1876: 11; type species: *Uroctonus mordax* Thorell, 1876, by original designation.

DIAGNOSIS. Comprises medium to large species, up to 60 mm in length; most species are dark mahogany in color, with contrasting darker carinae on metasoma and pedipalps. Orthobothriotaxic; ventral edge of cheliceral movable finger heavily crenulated with 4–7 denticles and distal edge exhibiting serrulae; movable finger of chelae with eight to nine internal denticles (ID); pedipalp patella with well-developed, double Dorsal Patellar Spur (DPS) and Ventral Patellar Spur (VPS); ventral carinae of sternite V and metasomal segments I–IV weak to well granulated, oriented essentially parallel on segments II–IV; carapace anterior edge with a conspicuous indentation, lateral eyes number three; dorsal lateral carinae terminus on metasomal segment V rounded, not flared; vesicular tabs present on telson vesicle, aculeus base on mature males not inflated; pectinal tooth counts range 11–15 in male, 8–12 in female; middle lamellae numerous and circular in shape.

DISTRIBUTION. USA (California, Oregon, Washington) (see map in Fig. 31).

REFERENCES (after Sissom, 2000):

Uroctonus: Thorell, 1877: 196; Karsch, 1879: 102–103 (in part); Pocock, 1893: 328; Thorell, 1893: 374; Kraepelin, 1894 (in part): 182, 193; Kraepelin, 1899: 182; Pocock, 1902: 5, 14; Ewing, 1928: 12; Hoffmann, 1931: 402; Werner, 1934: 283–284; Mello-Leitão, 1934: 81; Mello-Leitão, 1945: 128; Gertsch & Allred, 1965: 4; Gertsch & Soleglad, 1972: 553–568 (in part); Hjelle, 1972: 9 (in part); Soleglad, 1973: 351–360 (in part); Vachon, 1974: 914, 916; Stahnke, 1974: 119, 129–130, 132, Figs. 7A, 8A, 8B, Tab. 3, 4 (in part); Sissom, 1990: 111, 114 (in part), Figs. 3.19H, 3.19J; Williams & Savary, 1991: 272, 274, 284; Stockwell, 1992: 409, 416, 419, Figs. 47, 49, 51, 52, 53; Kovařík, 1998: 145; Sissom, 2000: 527–528.

TAXONOMIC HISTORY. Early authors (Karsch, 1879; Marx, 1890; Kraepelin, 1894) included in this genus also "*Uroctonus phaeodactylus*" which now is the type species of *Anuroctonus* (this, in fact, was a curious recognition of similarity between two uroctonine genera, later obscured by placing both in Vaejovidae and description of more vaejovid genera). Karsch (1879) also included in *Uroctonus* the third American species, *Uroctonus privus*, which is now a synonym of *Nullibrotheas allenii* (Chactidae) (Hjelle, 1972). The genus *Uroctonus* became monotypic since the monograph of Kraepelin (1899) and remained so until Gertsch & Soleglad (1972) described 13 new species. Stahnke (1974) moved of 12 of these species to genus *Vaejovis*; thus *Uroctonus* was reduced to only two species, *U. mordax* and *U. grahami*. One more species (*U. franckei*) was added by Williams (1986). However, Sissom (1990: 114) still considered *Uroctonus* to include 16 species. Sissom (2000) listed only three species in *Uroctonus*, all of which we recognize below. Recently, Soleglad & Fet (2003b) moved *Uroctonus* from Vaejovidae to Chactidae, under the resurrected subfamily Uroctoninae.

Sissom (2000: 527) incorrectly stated that the type species of *Uroctonus* was fixed by monotypy; in fact, it is a type species by original designation (Thorell, 1876); see ICZN (1999), Article 68.2.

Uroctonus mordax Thorell, 1876

Uroctonus mordax Thorell, 1876: 11.
Lectotype (designated by Hjelle, 1972: 15): female (NRS 59b), San Francisco, California, USA (see Comments).

DIAGNOSIS. Ventral carinae of metasomal segments II–IV distinctly granulated; carapace granular on lateral areas; median eyes small to medium but not noticeably reduced; overall color dark mahogany to yellow-brown, metasomal carinae slightly darker in color; fixed and movable fingers of chelae with seven to eight and eight to nine internal denticles (ID), respectively; setal formula of dorsal lateral carinae for metasomal segments I–IV is 1-2-2-2; length/width ratio of metasomal segments III–IV with median value 1.382/1.741 and 1.336/1.678 in male and female, respectively.

DISTRIBUTION. USA (California, Oregon, Washington) (see map in Fig. 31 and Comments).

SYNONYMS.

Vejovis yosemitensis Ewing, 1928: 11, Pl. II, Fig. 3 (synonymized by Gertsch & Soleglad, 1972: 568). Holotype: male (USNM), Yosemite Falls, Yosemite Valley, California, USA.

REFERENCES (after Sissom, 2000):

Uroctonus mordax: Mann, 1876: 212; Thorell, 1877: 196–198; Karsch, 1879: 102–103; Pocock, 1893: Pl. XIV, Fig. 15; Thorell, 1893: 374; Kraepelin, 1894: 194 (part); Kraepelin, 1899: 182, Fig. 57; Banks, 1900: 424; Kraepelin, 1901: 274; Pocock, 1902: 14–15, Pl. IV, Figs. 2, 2a–f; Banks, 1904: 365; Borelli, 1909: 224; Banks, 1910: 186, 188, Fig. 81e; Cox, 1921: 13; Ewing, 1928: 7, 15; Hoffmann, 1931: 402–403; Werner, 1934: 283–284; Mello-Leitão, 1945: 128; Gertsch & Allred, 1965: 4; Díaz Nájera, 1970: 116; Gertsch & Soleglad, 1972: 551, 565, 568–573, Figs. 1–9, 19, 28, 29, 40–51, 113–115, 119, 120, 133, 134; Soleglad, 1973: 353; Stahnke, 1974: 130; Vachon, 1974: Figs. 16(1), 78, 137; Williams, 1986: 359; Crawford, 1990: 258–259; Sissom, 1990: 104, 106, Fig. 3.18, 3.19H, 3.19J; Williams & Savary, 1991: 274, 284, Figs. 2, 6, 8, 14, 20; Kovařík, 1998: 145; Sissom, 2000: 528–529; Soleglad & Fet, 2003b: 102–103, Figs. 7, 9, 39, 81.

TAXONOMIC HISTORY. Hjelle (1972) described a new subspecies, *U. m. pluridens* from California. Sissom (2000: 529) and synonymized the long-forgotten subspecies ("form") *U. m. canaliculatus* Karsch, 1879.

COMMENTS. According to Sissom (2000: 529), two additional male specimens in Stockholm collection (NRS) should be regarded as paralectotypes.

The records for the southernmost Washington state (Klickitat and Skamania Counties) were published recently by Crawford (1990). Sissom (2000: 528-529) mentions also a record for Utah.

Table I. Morphometric ratio comparisons of *Uroctonus* species.
Metasoma segments I-V, Length/Width. Number of samples inside parentheses.

	I	II	III	IV	V
U. mordax					
♂ (3)	0.912–0.986	1.129–1.273	1.321–1.442	1.673–1.809	3.106–3.550
♀ (4)	0.922–0.938	1.100–1.286	1.228–1.444	1.519–1.837	2.750–3.174
U. franckei					
♂ (1)	1.000	1.400	1.679	2.200	3.696
♀ (2)	0.867–0.947	1.216–1.240	1.458–1.489	1.841–1.864	3.143–3.250
U. grahami					
♂ (-)	---	---	---	---	---
♀ (1)	1.000	1.294	1.563	2.000	3.357

Uroctonus mordax mordax Thorell, 1876
(Figs. 1, 3, 6, 12, 16, 18, 23, 26, 28, 32; Table I)

Uroctonus mordax Thorell, 1876: 11.
Lectotype (designated by Hjelle, 1972: 15): female (NRS 59b), San Francisco, California, USA (see Comments under *U. mordax*).

DIAGNOSIS. Ventral carinae of metasomal segments II–IV distinctly granulated; carapace granular on lateral areas; median eyes small to medium but not noticeably reduced; overall color dark mahogany, metasomal carinae slightly darker in color; fixed and movable fingers of chelae with seven and eight internal denticles (ID), respectively; setal formula of dorsal lateral carinae for metasomal segments I–IV is 1-2-2-2; length/width ratio of metasomal segments III–IV with median value 1.382/1.741 and 1.336/1.678 in male and female, respectively.

DISTRIBUTION. USA (California, Oregon, Washington) (see map in Fig. 31).

SYNONYMS.
Uroctonus mordax canaliculatus Karsch, 1879: 103 (synonymized by Sissom, 2000).
Holotype: male (ZMB 15), California, USA.

REFERENCES.
Uroctonus mordax mordax: Hjelle, 1972: 5, 12–19, Figs. 1–3, 7–9, 30, 32–36, 50, 52; Sissom, 2000: 529; Soleglad & Fet, 2003b: Figs. 9, 102.
Uroctonus mordax canaliculatus: Moritz & Fischer, 1980: 311.

SPECIMENS EXAMINED. USA: California: ***Humboldt County***: Weott, 21 September 1964 (Ivie), 1 adult male (MES); ***Kern County***: 0.25 miles N Alta Sierra, Sequoia National Forest (6,519 ft asl), (Lowe, Hébert), 1 adult male, 1 adult female (GL); ***Marin County***: 0.5 mi. SW Lagunitas, 3 September 1989, (Lowe), 3 adult males (GL); ***Mariposa County***: Foresta, Yosemite National Park, 3 August 1963 (Smoker), 1 adult male (MES); Big Meadow, Yosemite National Park, 12 July 1963 (Smoker), 2 adult females (MES); ***Trinity County***: McCray's Ranch, Burnt Ranch, 7 September 1980 (Lowe), 2 adult males (GL); Burnt Ranch, 25 December 1981 (Lowe), 1 adult male, 1 adult and 1 subadult female (GL).

COMMENTS. Gertsch & Soleglad (1972) described and illustrated this species in detail based on specimens from over 100 localities spanning Oregon and California (see their distribution map in Fig. 113). In their study, the trichobothrial patterns were illustrated for the first time. Hjelle (1972), whose study concentrated on the northern California coast ranges, investigated large samples of this species as well (spanning well over 70 localities), and conducted statistical analysis of the pectinal tooth counts, the number of denticles found on the ventral edge of the cheliceral movable finger, and the number of internal denticles (ID) found on the chelal finger. The latter investigation uncovered a new subspecies of *U. mordax* in the most southern part of its coastal California range (see below and map in Fig. 31).

Uroctonus mordax pluridens Hjelle, 1972
(Figs. 4, 14, 33; Table I)

Uroctonus mordax pluridens Hjelle, 1972: 5, 19–20, Figs. 37–40, 50, 52.
Holotype: male (CAS), near Corralitos, Santa Cruz County, California, USA.
Paratype: female (CAS; allotype), Scotts Valley, Santa Cruz County, California, USA.

DIAGNOSIS. Ventral carinae of metasomal segments II–IV distinctly granulated; carapace granular on lateral areas; median eyes small to medium but not noticeably reduced; overall color yellow-brown, metasomal carinae conspicuously darker in color; fixed and movable fingers of chelae with eight and nine internal denticles (ID), respectively; setal formula of dorsal lateral carinae for metasomal segments I–IV is 1-2-2-2; length/width ratio of metasomal segments III–IV with median value 1.382/1.741 and 1.336/1.678, in male and female, respectively.

DISTRIBUTION. USA (California) (see map in Fig. 31).

REFERENCES.
Uroctonus mordax pluridens: Kovařík, 1998: 145; Sissom, 2000: 529.

SPECIMENS EXAMINED. USA: California: ***Santa Cruz County:*** Big Basin, 21 July 1992 (Ramirez), 1 adult female (GL); ***Santa Clara County***: Santa Clara, June 1960, 1 adult male (MES).

COMMENTS. Hjelle (1972: 20, Figs. 50, 52) isolated this subspecies in the California counties of Santa Clara and

Santa Cruz, the most southern range of *Uroctonus* in coastal California; the description was based on eight males and fourteen females. This subspecies consistently possesses eight and nine internal denticles (ID) on fixed and movable fingers, respectively. In contrast, *U. m. mordax* has seven and eight. Intergrades between the two subspecies were also reported by Hjelle (1972), occurring where the ranges of two subspecies join. Due to the consistency of ID counts in scorpions in general, the isolated geographic range of *U. m. pluridens*, and the discovery of a hybrid population (i.e., only the movable finger reflecting an addition ID denticle), Hjelle's decision for subspecies status is correct.

***Uroctonus grahami* Gertsch & Soleglad, 1972**
(Table I)

Uroctonus grahami Gertsch & Soleglad, 1972: 565, 592–593, Figs. 15, 16, 26, 32, 33, 52–63.
Holotype: female (AMNH), Samwell Cave, Shasta County, California, USA.

DIAGNOSIS. Ventral carinae of metasomal segments II–IV essentially obsolete, other carinae smooth; pedipalps quite smooth with weak carinae; carapace generally smooth on entire surface; median eyes are noticeably reduced; overall color yellow to golden brown with little contrasting markings; metasoma somewhat elongated, length/width ratio of metasomal segments III–IV with median value 1.563 and 2.000 for the female. For a further description and illustrations of this species see Gertsch & Soleglad (1972: 592–593: Figs. 15, 16, 26, 32, 33, 52–55; Table VIII).

DISTRIBUTION. USA (California).

REFERENCES (after Sissom, 2000):
Uroctonus grahami: Soleglad, 1973: 353.
Uroctonus (?) *grahami*: Stahnke, 1974: 130.
Vaejovis grahami: Williams, 1976: 14; Kovařík, 1998: 147.
Uroctonus grahami: Reddell, 1981: 114; Williams & Savary, 1991: 284; Sissom, 2000: 528.

COMMENTS. This rare scorpion was described from three specimens all collected from Samwell Cave, Shasta County, California. It is unknown whether other specimens have been collected since its description in 1972. *U. grahami*, a somewhat small species (female type = 38.6 mm), is cave adapted exhibiting many attributes commonly found in cave scorpions, such as lighter coloration, more slender appendages, less granulation on the carapace, less developed pedipalp and metasoma carinae, and the reduction or loss of eyes. In Table I we see that *U. grahami* has the thinnest metasoma (only the female is shown) of all *Uroctonus* species, though this is based on a single set of measurements. Although cave adapted, *U. grahami* presents characters consistent with *Uroctonus*, such as the well-developed crenulation of the ventral edge of the cheliceral movable finger; the deeply notched anterior edge of the carapace; and the trichobothrial patterns of the chela, showing *ib-it* on the palm, below the fixed finger, V_1-V_2-V_3 juncture angling towards the internal aspect of the palm, and the *est-esb-eb* juncture angling towards the fixed finger dorsal edge, *eb* situated quite close to the articular membrane of the movable finger (see Gertsch & Soleglad, 1972: Figs. 52–55. Note that on the same page, in the Figs. 56–63, which illustrate the trichobothrial pattern of the patella of *U. grahami*, the species is *misidentified*; in actuality, it is the pattern of *Uroctonites huachuca,* fam. Vaejovidae).

***Uroctonus franckei* Williams, 1986**
(Figs. 19, 22; Table I)

Uroctonus franckei Williams, 1986: 359–362, Fig. 1.
Holotype: male (CAS, Type No. 15749), 17.7 km W Big Pine, Inyo County, California, USA.
Paratypes: 1 male, 3 females (CAS; including female allotype "type No. 15749"); same locality as holotype; 6 males (CAS), Oh Ridge Camp, June Lake, Mono County, California, USA; 2 females (CAS), 4.8 km E Whitney Portal, Inyo County, California, USA.

DIAGNOSIS. Ventral carinae of metasomal segments II–IV distinctly granulated; carapace granular on lateral areas; median eyes small to medium but not noticeably reduced; overall color dark mahogany, metasomal carinae slightly darker in color; fixed and movable fingers of chelae with seven and eight internal denticles (ID), respectively; setal formula of dorsal lateral carinae for metasomal segments I–IV is 1-1-1-2; length/width ratio of metasomal segments III–IV with median value 1.679/2.200 and 1.474/1.853, in male and female, respectively.

DISTRIBUTION. USA (California: eastern Sierra Nevada in Inyo & Mono Counties) (see map in Fig. 31).

REFERENCES (after Sissom, 2000):
Uroctonus franckei: Williams & Savary, 1991: 284; Kovařík, 1998: 145; Sissom, 2000: 528.

SPECIMENS EXAMINED. USA: California: ***Mono County*:** June Lake (10 mi. S Mono Lake), 23 August 1990, 1 subadult male, 1 adult female (GL).

COMMENTS. This species is based on a somewhat small isolated population found in the higher elevations of California's Sierra Nevada (over 2,000 m asl). Nine specimens were listed by Williams (1986: 361–362), four males and five females. In the original diagnosis, Williams (1986: 359) contrasts *U. franckei* with *U. mordax*: "… Related to *Uroctonus mordax* Thorell in size, structure, and coloration, but differs as follows: metasomal segments more slender, ratio of metasomal length to width of widest metasomal segment greater than 8.0; palm of chela more swollen, ratio of chela length to palm width 2.0 or greater; macrosetae along metasomal keels reduced in number, dorsolateral keels with macrosetal formula 1-1-1-2 on segments I–IV (not 1-2-2-2)…". We tested these characters, and, except for the setal formula, which in general complied, encountered difficulty with the other two diagnostic characters. Comparing the relative robustness of the chelae (which presumably implies it is both thicker and wider), we find the two species to be somewhat the same, *U. mordax* exhibiting smaller ratio values than *U. franckei*, implying it has a wider chelal palm. In addition, using the ratio of the metasomal length divided by the widest metasomal segment (which would be segment I), we see, using Williams published measurements of the holotype and allotype, that neither specimen complies with a value greater than 8.0 (i.e., this ratio as stated gives us values of 7.36 and 6.50 for male and female respectively). Therefore, going with Williams' general statement that the metasoma of *U. franckei* is thinner than in *U. mordax*, we measured all five metasomal segments and calculated straight length/width ratios for each segment (see Table I). This resulted in *U. franckei*, as reported by Williams, with a thinner metasoma, especially segments III–IV, which are reflected in our key. It must be stressed here, however, these differences in morphometric ratios are based on very limited data as reflected in Table I, and many more specimens of both species must be systematically measured in order to ascertain the overall consistency and therefore legitimacy of these ratios.

Genus *Anuroctonus* Pocock, 1893

Anuroctonus Pocock, 1893: 306, 309, 328–329; type species by original designation *Centrurus phaiodactylus* Wood, 1863 [=*Anuroctonus phaiodactylus* (Wood, 1863)].

DIAGNOSIS. Comprises small to large species, up to 80 mm in length, exhibiting both giant and dwarf races; species are light brown to dark mahogany in color, with contrasting darker pedipalpal fingers. Neobothriotaxic, major variable, Type *Ch3*; ventral edge of cheliceral movable finger weakly crenulated basally with 1–4 small denticles and distal edge lacking serrulae, but with a significant setal brush; movable finger of chelae with six internal denticles (ID); pedipalp patella with well developed single Dorsal Patellar Spur (DPS), Ventral Patellar Spur (VPS) vestigial; ventral carinae of sternite V and metasomal segments I–III noticeably raised from surface, broadly crenulate, and taper conspicuously in an anterior to posterior direction, carinae smooth to obsolete on segment IV; carapace anterior edge with a modest indentation, lateral eyes number four; dorsal lateral carinae terminus on metasomal segment V flared; vesicular tabs absent on telson vesicle, aculeus base on mature males conspicuously inflated; pectinal tooth counts range 6–12 in male, 4–9 in female; middle lamellae limited in number and rectangular in shape.

DISTRIBUTION. USA (California, southern Idaho, Nevada, Utah), Mexico (Baja California Norte) (see map in Fig. 31).

SYNONYMS.

Oncocentrus Thorell, 1893: 375; type species *Centrurus phaiodactylus* Wood, 1863 [=*Anuroctonus phaiodactylus* (Wood, 1863)], by original designation (synonymized by Kraepelin, 1899: 183).

REFERENCES (after Sissom & Fet, 2000; Sissom, 2000):

Anuroctonus: Laurie, 1896: 130; Kraepelin, 1899: 177, 183, Fig. 58; Pocock, 1902: 5, 13; Banks, 1910: 186; Penther, 1913: 247; Ewing, 1928: 14; Hoffmann, 1931: 403; Werner, 1934: 283–284; Mello-Leitão, 1945: 128; Gertsch, 1958: 14; Gertsch & Allred, 1965: 11; Williams, 1966: 419–428; Hjelle, 1972: 7–8; Gertsch & Soleglad, 1972: 564–565; Stahnke, 1974: 118; Vachon, 1974: 914, 936; Williams, 1974: 15; Anderson, 1975: 2–5, Figs. 1–4, 7, 12, Tab. 1; Williams, 1980: 14, Figs. 14–16; Francke & Soleglad, 1981: 235–245, Figs. 11, 15, 21, 38–41; Francke, 1985: 5, 18, 20; Sissom, 1990: 103, 112, 114, Figs. 3.6A–D, 3.19I; Nenilin & Fet, 1992: 9; Stockwell, 1992: 408, 419, Figs. 5, 64, 66; Kovařík, 1998: 135; Lourenço & Sissom, 2000: 118; Sissom & Fet, 2000: 413; Soleglad & Fet, 2003b: 104, Figs. 7, 10, 39, 82

Uroctonus (in part): Kraepelin, 1894: 196–198.

TAXONOMIC HISTORY.

Pocock (1893) established a monotypic genus *Anuroctonus*; the same was done independently by Thorell (1893) who established genus *Oncocentrus*. Kraepelin (1894) placed "*U. phaeodactylus*" in *Uroctonus*, but later (Kraepelin, 1899) accepted Pocock's genus. *Anuroctonus* was listed for a long time in Vaejovidae, as this family itself underwent major changes in volume and definition. Both Werner (1934) and Mello-Leitão (1934) included it into subfamily Uroctoninae, at that time listed under Vaejovidae. Stahnke (1974) placed *Hadrurus* and *Anuroctonus* together in subfamily Hadrurinae, still under Vaejovidae. When Francke & Soleglad (1981) moved *Hadrurus* to Iuridae, they thoroughly discussed *Anuroctonus* but decided not to include it in the Iuridae for a number of reasons. Sissom (1990: 114) listed *Anuroctonus* as "genus *incertae sedis*" outside of Chactidae and Vaejovidae, and noted (p. 103) that "The relationship of *Anuroctonus* to the other vaejovids is extremely unclear". Stockwell (1989, 1992) followed Stahnke (1974) in placing *Anuroctonus* in the Iuridae as the sister group of *Hadrurus*. Stockwell, however, did not fully address Francke & Soleglad's reasons for excluding *Anuroctonus* from the Iuridae. Nenilin & Fet (1992) suggested a separate vaejovid subfamily for *Anuroctonus* but did not provide any diagnosis. Sissom & Fet (2000) listed *Anuroctonus* under the Iuridae following Stockwell (1992) but commented that "the inclusion of *Anuroctonus* in the Iuridae should be regarded as tentative". Lourenço & Sissom (2000: 118) also tentatively accepted placement of this genus in Iuridae, and wrote that "further investigation seems to be warranted". Most recently, Soleglad & Fet (2003b) provided a detailed cladistic analysis of *Anuroctonus*, which supported its placement in Chactidae under Uroctoninae, as a sister group of *Uroctonus*.

Sissom & Fet (2000: 413) incorrectly stated that the type species of both *Anuroctonus* and *Oncocentrus* are fixed by monotypy; in fact, both are type species by original designation (Pocock, 1893; Thorell, 1893); see ICZN (1999), Article 68.2.

Anuroctonus was always thought to be monotypic. Here, we demonstrate that this genus in fact includes two species: the traditional *A. phaiodactylus* (Wood, 1863), and a new species, *A. pococki* **sp. nov**. The latter is further divided here in two subspecies (see below).

Table II. Morphometrics (mm) of *Anuroctonus phaiodactylus* (Wood).

	Utah 'Territory'	**Holbrook, Oneida Co., Idaho**	**Grantsville, Tooele Co., Utah**	**Stansbury Isl., Tooele Co., Utah**	**Coyote Spg., Lincoln Co., Nevada**	**Big Pine, Inyo Co., California**
	Male Type	**Male**	**Male**	**Female**	**Male**	**Male**
Total length	56.85	52.70	61.80	47.75	53.90	44.45
Carapace length	8.80	9.00	9.65	8.60	8.90	7.45
Mesosoma length	18.85	13.95	20.45	14.70	15.10	12.15
Metasoma length	21.35	21.35	23.10	18.65	21.60	18.05
Metasomal segment I						
length	2.50	2.60	2.85	2.20	2.60	2.30
width	3.45	3.50	3.90	3.10	3.40	3.05
Metasomal segment II						
length	3.15	3.20	3.35	2.80	3.15	2.80
width	3.15	3.40	3.45	2.75	3.20	2.80
Metasomal segment III						
length	4.10	3.90	4.30	3.55	4.00	3.30
width	2.85	3.25	3.25	2.65	3.05	2.60
Metasomal segment IV						
length	4.80	4.75	5.15	4.10	4.90	4.00
width	2.90	3.00	3.15	----	2.90	2.50
Metasomal segment V						
length	6.80	6.90	7.45	6.00	6.95	5.65
width	----	2.55	2.60	2.15	2.40	2.10
Telson length	7.85	8.40	8.60	5.80	8.30	6.80
width	3.45	3.65	3.90	2.10	3.45	3.25
depth	3.30	3.50	3.55	1.80	3.45	2.85
Pedipalp length	25.45	26.90	28.30	23.65	27.65	22.55
Femur length	5.45	5.85	6.30	5.35	6.10	5.05
width	2.40	2.50	2.60	1.90	2.50	2.20
Patella length	6.70	6.70	7.10	5.70	6.90	5.65
width	3.25	3.50	3.55	2.75	3.45	2.95
Chela length	13.30	14.35	14.90	12.60	14.65	11.85
Palm width	4.30	4.70	4.80	3.70	4.50	4.00
depth	5.45	5.85	5.95	4.60	5.75	5.05
Movable finger length	7.95	8.40	8.60	7.60	8.60	6.80

Anuroctonus phaiodactylus (Wood, 1863)

(Figs. 2, 7, 17, 27, 34, 41–42, 46, 48; Table II)

Centrurus phaiodactylus Wood, 1863a: 111.
Holotype: male (USNM, S-4, jar 2), Utah (description indicates "Utah Territory"; see description and comments below), USA.

DIAGNOSIS. Medium to large sized scorpion, carapace length of sexually mature males ranging 6.70–9.80 (8.210) (±0.589) [n = 177]. Light yellow to light brown in overall color, chelal fingers dark brown. Dorsal surface of carapace and mesosoma lacking heavy granulation. Ventral trichobothria of pedipalp chelae number 13–15 (14) (plus-minus standard error range and mean); digital carina (*D1*) of chelae weak to obsolete; interocular area of male carapace smooth; metasoma medium to slender, segment V length/width ratio 2.75–2.98 (2.86) and metasoma length/carapace length ratio 2.36–2.48 (2.42) for male (plus-minus standard error range and mean); ventroexternal carina (*V1*) of chelae pitted to irregularly granulate.

DISTRIBUTION. USA (eastern California, Idaho, Nevada, Utah). Distributed in the Great Basin: southern California, east of the Sierra Nevada and south to San Bernardino County; Nevada; Utah, west of the Wasatch Range of the Rocky Mountains; and extreme southern Idaho (see map in Fig. 31).

REFERENCES.

Centrurus phaiodactylus: Wood, 1863b: 372.

Uroctonus phaeodactylus (incorrect subsequent spelling): Karsch, 1879: 102, 103; Marx, 1890: 91; Kraepelin, 1894: 196–198.

Anuroctonus phaeodactylus (incorrect subsequent spelling): Pocock, 1893: 309, 328–329, Pl. XIV, Figs. 14–15; Laurie, 1896: 122; Kraepelin, 1899: 183; Pocock, 1902: 13–14 (in part), Pocock, 1902: 13–14 (in part); Plate IV, Fig. 1 (San Bernardino); Cox, 1921: 13 (in part); Werner, 1934: 284; Gertsch & Allred, 1965: 11–12, Figs. 16–20 (in part); Williams & Hadley, 1967: 112; Johnson & Allred, 1972: 157; Stahnke, 1974: 127–129 (in part); Vachon, 1974: Figs. 16(3), 143, 146, 157–159.

Oncocentrus phaeodactylus (incorrect subsequent spelling): Thorell, 1893: 375.

Uroctonus phaiodactylus: Banks, 1900: 424 (in part).

Anuroctonus phacodactylus (incorrect subsequent spelling): Kraepelin, 1901: 274.

Anuroctonus phaiodactylus: Banks, 1910: 188 (in part); Ewing, 1928: 14–15 (in part); Anderson, 1975: 2–5, Figs. 1–4, 7, 12, Tab. 1; Williams, 1980: 14–15, Figs. 14–16 (in part); Francke & Soleglad, 1981: 238, Figs. 11, 15, 21, 38–41; Kovařík, 1998: 135 (in part); Lourenço & Sissom, 2000: 118 (in part); Sissom & Fet, 2000: 414 (in part).

TAXONOMIC HISTORY. Hjelle (1972: 8) emphasized that the spelling of specific epithet should be "*phaiodactylus*", stating that Karsch (1879) changed the original spelling to "*phaeodactylus*" without a justification.

Here, the scope of *A. phaiodactylus* is restricted as we describe another species based on populations previously included in *A. phaiodactylus*. We marked "in part" those references which allow distinguishing localities of *Anuroctonus phaiodactylus* from those of *A. pococki* (see map in Fig. 31); see also references under *A. pococki*. Note that all localities from Mexico and western California belong to *A. pococki*.

MALE (holotype; see measurements in Table II). We describe here only species-level diagnostic characters as established in this paper. Holotype is deposited in USNM, general locality given as "Utah Territory, USA". Holotype is a sexually mature male, exhibiting the "hallmark" swollen base of the telson aculeus. The overall specimen, 56.85 mm in length, is in reasonably good shape, but somewhat desiccated; overall coloration a dark brown, presumably due to prolonged preservation. Carapace interocular area smooth, with a few small granules on extreme anterior edge; tergites generally smooth, with slight roughness detected at 20x; chelal digital (*D1*) carina obsolete to rounded; V1 carina well developed, rough to irregularly granulated and pigmented; chelal ventral trichobothria number 15–16, left and right chelae, respectively; metasomal length (21.35) divided by carapace length (8.8) = 2.426; pectinal teeth 8–9.

It is clear from the presumed geographic locality (see below), ventral trichobothria counts of the chelae (15–16), the relatively smooth carapace interocular area, the weakly developed digital (*D1*) carina, and the morphometric ratio based on the metasoma length/carapace length (= 2.426), that the holotype male specimen is consistent with the Great Basin populations of *Anuroctonus* identified herein as *A. phaiodactylus*. See Figure 34 for a dorsal view of the male of this scorpion species.

LOCALITY OF HOLOTYPE. One faded label inside vial: *C. phaiodactylus* Utah; outside label: U. S. National Museum Collection, TYPE 2, S-4, *Centrurus phaiodactylus* C. H. Wood. Horatio C. Wood (1863) recorded type specimen locality as "Utah Territory", collector M. McCarthy, presumably circa 1860. Utah Territory was established in 1848 after the land was acquired officially by the United States following the Treaty of Guadalupe Hidalgo after the Mexican War (New Columbia Encyclopedia). This large area included the present states of Utah, Nevada, Colorado, and Wyoming. In 1861, this area was reduced by the creation of the Nevada and Colorado territories, and in 1868, the area was further reduced by the creation of the Wyoming territory (the remaining area, Utah, reached statehood in 1896). The collection date of the type specimen is not stated, however, we assume here it is circa 1860, which seems reasonable since the Wood's paper was published in 1863. Therefore, we can assume that Utah Territory in this context included all four states. However, if the collection occurred after the creation of the Nevada and Colorado territories (1861), then its locality determination is reduced to two states, only one, Utah, as an obvious choice for the type specimen's locality. As a minimum, we know that *A. phaiodactylus*, as identified herein, is found in both Nevada and Utah, therefore we can presume from this data that the type specimen is from either one of these two states (to our knowledge, *Anuroctonus* has not been reported from Colorado or Wyoming).

FEMALE. The sexually mature male is distinguished from the female by its conspicuous swollen telson vesicle and aculeus base. The genital operculum sclerites of both genders are separated for most of their length, a typical chactid attribute; however, the male exhibits genital papillae which are essentially covered by the plates. The inner proximal edges of the plates in the female are more rounded than in the male. The individual pecten of the male is longer, the teeth more developed, and the sensory areas cover a larger area of the tooth. Pectinal tooth counts are as follows: male = 6–12 (8.50) (±0.80) [311]:{8–9}→ 0.094; female = 5–9 (6.90) (±0.79) [039]:{6–8}→ 0.114 (see Fig. 37).

SPECIMENS EXAMINED. USA: California: ***Inyo County:*** 2.9 mi. NE. Big Pine (4,080 ft asl), 20 August 1990 (Lowe, Williams), 2 males (GL); Coso Village (NAWS), 22 June–10 August 1996 (Pratt, Pierce), male (UCR); Coso Village (NAWS), 10 August–14 September 1996 (Pratt, Pierce), male (UCR); Falls Creek (5,500 ft asl), November 1970 (Giuliani), male (CAS); Haiwee Canyon, 19 January 1972 (Giuliani), female (CAS); Grapevine Canyon Rd., Saline Valley (5,850 ft asl), 14 June 1960 (Banta), male (CAS); Grapevine Canyon Rd., Saline Valley (4,480 ft asl), 15 August 1959 (Banta), male (CAS); Grapevine Canyon Rd., Saline Valley (5,320 ft asl), 15 August 1959 (Banta), male (CAS); Grapevine Canyon Rd., Saline Valley, 7 May 1960 (Banta), male (CAS); Grapewine Canyon Rd., Saline Valley (5,570 ft asl), 15 August 1959 (Banta), male (CAS); Grapewine Canyon Rd., Saline Valley, 27 August 1965 (Lee), male (CAS); Grapewine Canyon Rd., Saline Valley, 14 June 1960 (Banta), male (CAS); Grapewine Canyon Rd., Saline Valley (5,700 ft asl), 15 August 1959 (Banta), male (CAS); Grapewine Canyon Rd., Saline Valley (5,100 ft asl), 15 August 1959 (Banta), male (CAS); Grapewine Canyon Rd., Saline Valley (5,750 ft asl), 4 July 1959 (Banta), male (CAS); Saline Valley, 2 May 1959 (Banta), male (CAS); ***Kern County:*** Bird Spring Canyon Rd., 3 August 1997 (Lowe, Hébert), male, subadult female (GL); Jawbone Canyon Rd., 1 August 1997 (Lowe, Hébert), male (GL); Kelso Valley Rd., 3 August 1997 (Lowe, Hébert), 2 males (GL); Nine Mile Canyon Rd., to Kennedy Flat, 2 August 1997 (Lowe, Hébert), 3 males, female (GL); Nine Mile Canyon Rd. to Chimney Peak campground, 2 August 1997 (Lowe, Hébert), male; Nine Mile Canyon Rd. to Chimney Peak campground, 2 August 1997 (Lowe, Hébert), 7 males (GL); 20 mi. E Weldon, 5.9 mi. W Rte 14, 5 June 1971 (Haradon), subadult male, 6 females (CAS); ***San Bernardino County:*** Caruther Caverns, New York Mountains, 25 July 1978 (Vitt), male (WDS).

Idaho: ***Oneida County:*** 3 mi. NW Holbrook (4,000 ft asl), May–September 1968–1974 (Anderson, Rhoades), 40 males, female (RA); 5 mi. NE. Holbrook (4,000 ft asl), 1 August 1969 (Anderson), adult male (AMNH).

Nevada: ***Churchill County:*** 60 mi. E Fallon, off Hwy 50, 15 August 1969 (Miller), male (USNM); ***Lincoln County:*** 5 km N. Coyote Spr. (5,200–5,400 ft asl), 15 August 1990 (Lowe), 4 males (GL); 12.9 mi. NW. Pioche (5,440 ft asl), 15 August 1990 (Lowe, Williams), male and female (GL); ***Mineral County:*** 3.3 km N. Thorne (4,500–4,600 ft asl), 10 August 1990 (Lowe, Williams), male (GL); ***Nye County:*** 7.4 SW. Belmont (6,550 ft asl), 12 August 1990 (Williams, Bechtel, Lee, Chinn, Lowe), female (CAS); Mercury (Nevada Test Site), 29 March 1960 (collector unknown), female (BEAN); Mercury (Nevada Test Site), 14 August 1960 (collector unknown), male (BEAN); Mercury (Nevada Test Site), 24 August 1964 (Allred), male (BEAN); Mercury (Nevada Test Site), 2 August 1960 (collector unknown), male (BEAN); Sarcobatus Flat, 10 February 1974 (Giuliani), female (CAS); 4.2 mi. SE Stonewall Pass (4,575 ft asl), 4 August 1955 (Banta), male (CAS); 8 Mi. NE Stonewall Jct. (5,350 ft asl), 4 August 1955 (Banta), male (CAS); ***White Pine County:*** 3.2–3.7 mi. E. Baker (5,900 ft asl), 8 August 1994 (Williams, Bechtel), 2 females (CAS); 4.1 mi. E. Baker (6,600 ft asl), 8 August 1994 (Williams, Bechtel), male (CAS); 4.2 mi. E. Baker (5,500 ft asl), 8 August 1994 (Williams, Bechtel), 3 females (CAS).

Utah: ***Beaver County:*** 31 mi. SE Garrison, 26 May 1994 (J. Van Zee), 10 males (JVZ); Milford, 29 June 1945 (Shelford), adult male (AMNH); ***Box Elder County:*** Grouse Creek, 7 July 1968 (Johnson), 14 males (BEAN); Lucin, 7 July 1968 (Johnson), subadult female (BEAN); *Iron:* Cedar City, 4 June 1968 (Johnson), 5 males (BEAN); ***Millard County:*** Clear Lake, 3 June 1968 (Johnson), 1 subadult and 13 adult males (BEAN); 15 mi. SE Garrison, 26 May 1994 (J. Van Zee), 4 males (JVZ); 19 mi. SE Garrison, 17 May 1994 (J. Van Zee), 10 males (JVZ); 28 mi. SE Garrison, 15 May 1994 (J. Van Zee), 4 males (JVZ); 28 mi. SE Garrison, 29 May 1994 (J. Van Zee), 5 males (JVZ); 38 mi. SE Garrison, May 1994 (J. Van Zee), 6 males (WDS); Holden, 1 June 1968 (Johnson), male (BEAN); ***Tooele County:*** 3 mi. W. Grantsville (5,200 ft asl), August 1970 (Brown), 15 males and 2 juveniles (CAS); Knolls, 5 July 1968 (Johnson), male (BEAN); Stansbury Island, 4–13 May 1993 (Stockwell), adult and 3 subadult males, female (USNM); ***Utah County:*** Cedar Valley, 30 May 1968 (Camenzind), male (BEAN); Provo, 10 August 1962 (collector unknown), male (BEAN); Provo, 15 July 1951 (Beck), male (BEAN); Spanish Fork, 30 May 1928 (Beck), female (BEAN); Springville, no date (Finley), male (BEAN); ***Washington County:*** Curley Hollow Wash (3,350–3,400 ft asl), 26 August 1992 (Lowe, Icenogle), 3 males (GL); Hurricane, 5 July 1931 (Gertsch), adult female (AMNH).

Utah Territory (= Nevada, Utah, Colorado, and Wyoming): circa 1860 (McCarthy), male (**holotype**) (USNM).

Anuroctonus pococki Soleglad & Fet, sp. nov.

HOLOTYPE: male, 1 mi. north of Santee, San Diego County, California, USA, collector M. E. Soleglad, 18 September 1970 (CAS). **Paratypes:** 1 mi. N. Santee, 18 September 1970 (Soleglad), 1 adult male (MES); 1 mi. N. Santee, 19 February 1972 (Soleglad, Erickson), male and female juveniles (MES); 1 mi. N. Santee, 16 April 1973 (Soleglad, Erickson), adult male (MES).

DIAGNOSIS. Small to large sized scorpion, exhibiting dwarf as well as large races, carapace length of sexually mature males ranging 6–12 (7.952) (±0.912) [135]. Light yellow to almost black in overall color, chelal fingers dark brown to black. Dorsal surface of carapace and mesosoma exhibiting medium to heavy granulation. Ventral trichobothria of pedipalp chelae number 16–20 (18.025) (plus-minus standard error range and mean); digital carina (*D1*) of chelae well-developed; interocular area of male carapace granular; metasoma slender, segment V length/width ratio 2.98–3.25 (3.112) and metasoma length/carapace length ratio 2.49–2.67 (2.584) for male (plus-minus standard error range and mean); ventroexternal carina (*V1*) of chelae smooth to distinctly granulated.

DISTRIBUTION. USA (California), Mexico (Baja California Norte) (see map in Fig. 31).

REFERENCES:

Uroctonus phaiodactylus: Banks, 1900: 424 (in part); Banks, 1904: 365.

Anuroctonus phaiodactylus: Banks, 1910: 188 (in part); Ewing, 1928: 14–15 (in part); Hjelle, 1972: 5, 7–8; Díaz Nájera, 1975: 8; Williams, 1980: 14–15, Figs. 14–16 (in part); Sissom, 1990: 72, Fig. 3.6; Kovařík, 1998: 135 (in part); Lourenço & Sissom, 2000: 118 (in part); Sissom & Fet, 2000: 414 (in part); Beutelspacher, 2001: Tab. 13A–E.

Anuroctonus phaeodactylus (incorrect subsequent spelling): Pocock, 1902: 13–14 (in part); ?Penther, 1913: 247; Cox, 1921: 13 (in part); Hoffmann, 1931: 404–405; Passmore, 1938: 94; Gertsch, 1958: 14 (in part); Gertsch & Allred, 1965: 11–12, Figs. 16–20 (in part); Williams, 1966: 419–428; Díaz Nájera, 1970: 116; Stahnke, 1974: 127–129 (in part); Díaz Nájera, 1975: 8.

Anuroctonus sp.: Soleglad & Fet, 2003b: Figs. 34, 103.

Anuroctonus pococki pococki Soleglad & Fet, ssp. nov. (Figs. 21, 25, 29, 35, 38, 43; Table III)

HOLOTYPE. Same as in *A. pococki*; see description below. **Paratypes:** Same as in *A. pococki.*

DIAGNOSIS. Medium to large sized scorpion, exhibiting large races, carapace length of sexually mature males ranging 7.20–12.00 (8.564) (±0.952) [n = 54]. Light yellow to almost black in overall color, chelal fingers dark brown to black. Dorsal surface of carapace and mesosoma exhibiting medium to heavy granulation. Ventral trichobothria of pedipalp chelae number 17–21 (19.233) (plus-minus standard error range and mean); digital carina (*D1*) of chelae well developed and pigmented; interocular area of male carapace granulose; metasoma slender, segment V length/width ratio 2.98–3.27 (3.13) and metasoma length/carapace length ratio 2.45–2.56 (2.51) for male (plus-minus standard error range and mean); ventroexternal carina (*V1*) of chelae generally smooth.

DISTRIBUTION. USA (southern coastal California, north to Monterey County and west of the Sierra Nevada), Mexico (extreme north coastal Baja California Norte) (see map in Fig. 31).

ETYMOLOGY. This scorpion species is named in honor of the famous British zoologist Reginald Innes Pocock (1863–1919) whose contributions to scorpion taxonomy still have widespread influence on today's existing systematics.

MALE. Description based on holotype male permanently deposited in CAS. Locality of holotype is 1 mi. north of Santee, San Diego County, California, USA; collector M. E. Soleglad, 18 September 1970. Measurements of this type specimen plus other material presented in Table III. See Fig. 35 for a dorsal view of the male of this species.

Table III. Morphometrics (mm) of *Anuroctonus pococki pococki* sp. nov.

	Santee, San Diego Co., California	Mt. Sally, Los Angeles Co., California	Winchester, Riverside Co., California	Wrightwood, San Bernadino Co., California	Fallbrook, Riverside Co., California	San Dimas Cyn., Los Angeles Co., California
	Male Type	Male	Male	Male	Male	Female
Total length	57.50	52.25	66.15	58.05	55.90	57.30
Carapace length	8.70	8.70	11.40	8.70	8.90	10.70
Mesosoma length	18.85	12.80	15.20	17.20	17.20	21.65
Metasoma length	22.10	22.45	28.95	24.00	22.25	24.95
Metasomal segment I						
length	2.50	2.60	3.45	2.90	2.70	3.00
width	3.55	3.65	4.60	3.75	3.65	4.15
Metasomal segment II						
length	3.15	3.35	4.20	3.55	3.30	3.55
width	3.30	3.30	4.20	3.30	3.35	3.75
Metasomal segment III						
length	3.95	4.25	5.25	4.45	4.20	4.60
width	3.20	3.05	4.00	3.15	3.10	3.60
Metasomal segment IV						
length	5.05	4.90	6.30	5.35	4.70	5.60
width	2.95	2.90	3.55	2.95	2.90	3.40
Metasomal segment V						
length	7.45	7.35	9.75	7.75	7.35	8.20
width	2.35	2.40	2.95	2.45	2.20	2.80
Telson length	8.05	8.30	10.60	8.15	7.55	8.60
width	3.25	3.35	4.20	3.70	3.35	2.90
depth	3.50	3.60	4.50	3.55	3.05	2.85
Pedipalp length	27.50	26.50	35.90	27.90	26.50	29.45
Femur length	5.95	5.75	7.85	6.15	5.65	6.40
width	2.60	2.50	3.35	2.55	2.60	2.50
Patella length	7.00	6.60	9.00	7.00	6.70	7.45
width	3.65	3.45	4.60	3.55	3.55	3.60
Chela length	14.55	14.15	19.05	14.75	14.15	15.60
Palm width	4.80	4.60	6.50	4.80	4.60	5.40
depth	6.05	5.65	8.05	5.85	5.55	6.45
Movable finger length	8.05	8.15	10.60	8.30	7.75	8.80

Coloration. Basic color tan to medium brown. Carapace and mesosoma dark brown, metasoma light brown, telson brown-orange, aculeus, eyes and eye tubercles dark brown to black. Pedipalps brown, chelal fingers reddish at base, black distally, carinae dark brown to black. Legs yellow, articulation condyles dark brown to black.

Carapace. Anterior edge with subtle indentation; wide, deep indentation bisecting interocular area which is covered with large granules, posterior lateral aspects exhibiting slight granulation. Lateral eyes number four, small fourth eye positioned above the most posterior eye. Median eye tubercle thin, positioned anteriorly of the middle with the following length and width formulas: 380|870 (anterior edge to medium tubercle middle|carapace length) and 90|640 (width of median tubercle|width of carapace at that point).

Mesosoma. Tergites I–VI smooth to rough at 10x; tergite VII covered with coarse granules, obscuring median and lateral median carinae, the latter only visible on extreme posterior aspect. Sternites smooth; ventral lateral and median carinae very well developed on sternite V, broadly crenulate and highly tapered in an anterior to posterior direction (i.e., not parallel), corresponding to same well-developed carinae exhibited in metasomal segments I–III. Stigmata of medium length, thin oval-shaped.

Metasoma. Segments I–IV: dorsal and dorsal lateral carinae delicately granulated; lateral carinae granulated on basal half of I, proximal 40% of II, and essentially obsolete on III–IV; ventral lateral and median carinae of I–III exaggerated, highly raised from segment and broadly crenulate, tapering in an anterior to posterior direction, as that described for the two carinal pairs on sternite V; ventral lateral smooth and ventral median obsolete on IV. Segment V: dorsal lateral carinae delicately granulated; lateral granulated for 50% of anterior aspect; ventral lateral and median carinae serrulate, median bifurcated posteriorly, exhibiting a Y-shaped pattern. Intercarinal areas smooth. Dorsal lateral carinae of segment IV terminate directly at articulation condyle, not flared; extreme dorsal posterior aspect of segment V is highly flared.

Telson. Vesicle highly inflated laterally, juncture with aculeus exhibiting a swollen “bulb”, indicative of a sexually mature male. Vesicle surface smooth and shiny, basal dorsal aspect without vesicular “tabs”.

Pectines. Short wide segments exhibiting length|width formula 270|160 (length taken at anterior lamellae|width at widest point including teeth). Sclerite construction simplistic, three anterior lamellae and one middle lamellae, abutted to basal anterior lamella; fulcra of medium development. Teeth number 9/9. Sensory areas well-developed along most of tooth inner length. Basal piece elongated, no indentation, length|width formula 240|100.
Genital Operculum. Sclerites separated for most of length; genital papillae present but do not extend beyond posterior edge of plates.
Sternum. Type 2, deep posterior emargination present, well-defined convex lateral lobes, slightly wider than long, length|width formula 225|250.
Chelicerae. Appendages elongated, denticles are somewhat worn down. Movable finger dorsal edge with two subdistal (*sd*) denticles; movable edge with one very blunt, small and worn denticle on basal half; basal half with heavy setal brush, serrulae absent. Ventral distal denticle (*vd*) considerably longer than dorsal (*dd*) counterpart. Fixed finger with four denticles, median (*m*) and basal (*b*) denticles conjoined on common trunk.
Pedipalps. Heavily chelate species, little or no scalloping on chelal fingers, thus not exhibiting sexual dimorphism in this structure. **Femur:** Dorsal internal, external, and ventral internal carinae equipped with large serrulate granules; ventral external rounded to obsolete. Dorsal surface rough, large granules present on proximal area; ventral surface with heavy granulation on proximal half; internal surface with heavy granulation on ventral half; external face smooth. **Patella:** Internal carinae with large serrulate granules; dorsal external carina smooth to obsolete; ventral external rounded and rough; exteromedian obsolete. All surfaces smooth; internal surface with a large well developed Dorsal Patellar Spur (DPS), Ventral Patellar Spur (VPS) quite small, represented by a solitary granule. **Chelal carinae:** digital (*D1*) carina strong, smooth and pigmented; subdigital (*D2*) represented basally by two large granules; dorsosecondary (*D3*) weak and rounded; dorsomarginal (*D4*) and dorsointernal (*D5*) rounded, irregularly granulose, the latter somewhat weak; ventroexternal (*V1*) strong, smooth and pigmented, curving distally towards midpoint between movable finger condyles (internal of trichobothrium Et_1); ventromedian (*V2*) weak and rounded, with large granules on proximal one-quarter; ventrointernal (*V3*) strong, rounded, irregularly granulated; external (*E*) rounded with slight granulation on proximal one-third.
Chelal finger dentition: median denticle (MD) row groups aligned in straight line; 5/5 and 6/6 internal denticles (ID) and 6/6 and 7/7 outer denticles (OD) on fixed and movable fingers, respectively. Basal outer denticle of movable finger slightly enlarged. No accessory denticles. **Trichobothrial patterns (**Fig. 29**):** Type C, neobothriotaxic (major additive) type *Ch3* (defined in Soleglad & Fet, 2003b: 50) on chela and patella. Femur: trichobothrium *d* located next to dorsoexternal carina and adjacent to *i*. Patella: 23 ventral trichobothria (16 ventral and 7 "wrap-around" on external surface), most proximal petite; *eb* = 7, *est* = 2, *em* = 7, *est* = 4, and *et* = 3. Chela: 24/26 ventral trichobothria.
Legs. Both pedal spurs present, tibial spurs absent. Tarsus with single median row of spinules on ventral surface, terminating distally with a single spinule pair.
Hemispermatophore. See Fig. 27 for structure in the genus.

FEMALE. Sexual dimorphism as discussed for *A. phaiodactylus* is reflected in this subspecies. Pectinal tooth counts: male = 6–11 (8.77) (±0.88) [141]: {8–10}→ 0.101; female = 4–9 (6.88)(±1.01) [120]: {6–8}→ 0.146 (see Fig. 37).

SPECIMENS EXAMINED:

USA: Arizona [??]: ***Coconino County:*** "Bill Williams Fork", August 1903 (Snow), male (CAS-S).
California: ***Contra Costa County*** **[??]:** Richmond, August 1952 (collector unknown), male (CAS-S); ***Kern County:*** 10 mi. NE Bakersfield, 28 June 1985 (Stockwell, Taber), 2 females (WDS); Sequoia National Forest, 28 July 1985 (Stockwell), subadult and juvenile females (USNM); Sequoia National Forest, 28 June 1985 (Stockwell), adult and 3 subadult males, female (USNM); Banducci Rd. N Tehachapi Mtn., 5 August 1997 (Lowe, Hébert), male (GL); 20 SE. Tehachapi, 19 June 1987 (Lowe), female (GL); ***Los Angeles County:*** Angeles Forest Hwy (5,000 ft asl), 25 July 1981 (Lowe), juvenile (GL); Big Pines Hwy, 1 mi. W Cauldwell Lake, 27 June 1982 (Hébert), subadult female (BH); Crystal Lake, 29 June 1950 (Bentinck), male (USNM); Angeles Crest Hwy, George Gap (5,000 ft asl), 27 June 1985 (Lowe), male (GL); Los Angeles, 7 January 1934 (collector unknown), male (BEAN); Los Angeles, 19 April 1936 (Grant), male, female (WDS); Manker Flats, Mount Baldy (6,100 ft asl), 15 April 1987 (Lowe), female (GL); Angeles Crest Hwy, Mt. Sally (5,000 ft asl), 27 June 1982 (Lowe), male (GL); San Dimas Cyn., 23 January 1971 (Jillson), adult male (AMNH); ***Monterey County:*** Carmel Valley, 7 November 1963 (Johnson), juvenile female (CAS-S); Gonzales, 24 June 1963 (Johnson), female (CAS-S); Los Padres National Forest, 4 mi. SE Nacimiento Summit Campground, 8 August 1970 (Azeuedo, Lee), male (CAS); Marina, Ft. Ord, 24 July 1969 (blank), adult male (AMNH); Paloma Canyon, 40 mi. from Monterey, 16 December 1963 (Johnson), female (CAS-S); Paloma Canyon, 40 mi. from Monterey, 25 December 1963 (Johnson), female (CAS-S); S Monterey, 8 April 1972 (Johnson), male, subadult female (CAS-S); ***Orange County:*** Several mi. E El Toro, 16 January 1971 (Haradon, Marks), 1 juvenile and 1 adult male, 2 females (CAS); 0.5 mi. NE Laguna Beach, Rte 518, 21 February 1972 (Haradon, Marks), subadult male, 1 juvenile, 3 subadult, and 6 adult females (CAS); ***Riverside County:*** Fisherman's Cmp., 19 February 1983 (Lowe), female (GL); Fishermen's Cmp., 23 March 1984 (Lowe), female (GL); Garner Valley, 5 mi. S Hwy 74, 26 April 1980 (Bethke), male (UCR); Hemet, Hwy 74, 23 October 1983 (Hébert), male, female (BH); 7 mi. N Idyllwild, 27 June 1989 (Bethke), juvenile and adult female (UCR); Idylwild (5,400 ft asl), June 1921 (Miller), male (USNM); Menifee Valley, 27 June 1993 (Frommer), subadult female (UCR); Norco, 7 July 1990 (Sanborn), male (UCR); San Juan Cmp., 23 March 1983 (Lowe), female (GL); Winchester, 8 February 1983 (Lowe, Icenogle), male (GL); Winchester, 9 October 1981 (Icenogle), 8 juveniles (GL); Winchester, 24 June 1982 (Icenogle), female (USNM); ***San Benito County:*** 25 E. Pinnacles National Monument, 12 October 1970 (Hitch), male (CAS); Pinnacles National Monument, 23 March 1968 (Williams), female (CAS); Pinnacles National Monument, 17 June 1972 (Larrea, Floyd), male (CAS); Pinnacles National Monument, 24 October 1970 (Williams), female and 5 juveniles (CAS); ***San Diego County:*** DeLuz Rd., 0.5 mi. N. Fallbrook, 25 August 1984 (Lowe), 2 males and 3 females (GL); Fallbrook, 26

June 1982 (Lowe), male (GL); La Jolla, 4 July 1921 (Cook), male (USNM); Mission Gorge, 25 October 1986 (Stockwell), adult and subadult males, female (USNM); Mission Gorge, 5 September 1987 (Stockwell), male and female (USNM); Mission Valley, 30 March 1988 (Stockwell, Brown), female (USNM); DeLuz Rd., 8 mi. SW Murietta, 19 February 1983 (Lowe), male (GL); San Diego, 1884 (Orcutt), male (USNM); 1 mi. N. Santee, 18 September 1970 (Soleglad), 2 adult males (MES); 1 mi. N. Santee, 16 April 1973 (Soleglad, Erickson), adult male (MES); 1 mi. N. Santee, 19 February 1972 (Soleglad, Erickson), male and female juveniles (MES); Sorrento Valley Blvd., October 1978 (Soleglad), adult male (MES); between Temecula and Pala, 12 February 1929 (Cook), male (USNM); Witchcreek, no date (Henshaw), female (USNM); Witchcreek, no date (no collector), female (USNM); ***San Luis Obispo County:*** 2 mi. E. San Luis Obispo, 26 December 1966 (Wong), female (CAS); 2 mi. E. San Luis Obispo, 26 December 1966 (Hom), male (CAS); San Luis Obispo, 29 July 1965 (Burnett), male (CAS-S); ***Santa Barbara County:*** Buellton, 22 June 1947 (collector unknown), male (CAS-S); 6 mi. N Lompoc, 15 February 1962 (Simonds), female (CAS-S); ***Tulare County:*** 7.8 mi. N Kernville Rt 190 (Kern County), 12 June 1971 (Haradon, Marks), male, 1 subadult and 2 adult females (CAS); ***Ventura County:*** Deer Creek Rd., 8 August 1997 (Lowe, Hébert), male (GL); Frazier Mtn. Rd., 6 August 1997 (Lowe, Hébert), adult, subadult, juvenile males (GL); Frazier Mtn. Rd., male (JB); Santa Monica Mtn., Sycamore Canyon Rd., 16 August 1971 (Haradon, Marks), male (CAS); Santa Monica Mtn., Sycamore Canyon Rd., 27 December 1970 (Haradon), 2 juveniles (CAS); Santa Monica Mtn., Yerba Buena Rd., 18 August 1971 (Haradon), male and 2 females (CAS); Santa Monica Mtn., Yerba Buena Rd., 14 May 1972 (Haradon, Marks), male (CAS); Valle Vista Cmp. (2,500 ft asl), 9 October 1982 (Lowe), female (GL); Yerba Buena Road, inter. Yellow Hill and Serrano roads, 8 November 1991 (Powell), 1 juvenile male, 1 female (WDS); Yerba Buena Road, between Yellow Hill and Serrano roads (Powell), female (WDS); Yerba Buena Rd., 3 mi N Rte 1, 8 August 1997 (Lowe, Hébert), 3 males (GL).

MEXICO: **Baja California Norte:** 5 mi. S. La Mision (500 ft asl), 14 April 1969 (Williams), female (CAS); 17 mi. S. Santo Tomas, 31 August 1957 (Roth), adult male (AMNH). **Oaxaca [??]**: San Geronimo, July 1909 (Petrunkevitch), adult male and female (AMNH).

DISCUSSION: We discuss the three questionable locality records for *A. p. pococki* listed above:

Contra Costa Co., California, CAS-Stahnke collection. Vincent Lee (CAS) had this to say (pers. comm., September 1996) about the possibility of *Anuroctonus* being found in Contra Costa Co.: "…Richmond does not seem to have the proper habitats for *A. phaiodactylus* (I'm in agreement with Warren [he is referring to Warren Savary]). Primarily for this reason and secondarily for the fact that I've found errors in transcription (i.e., retyping of original labels) by Stahnke and/or his students, etc., lead me to suspect incorrect locality data. …". We accept Lee's opinion here and therefore consider this locality to be spurious. The specimens certainly are consistently with *A. p. pococki*, however, we suspect they originated somewhere from southern coastal California.

Coconino Co., Bill Williams Fork, August 03 (1903?), from the F.H. Snow Entomological Museum, ASU65-0076. If this locality is correct, then it represents the first report of *Anuroctonus* for Arizona. Joe Bigelow, who studies Arizona scorpions extensively, reports (pers. comm., August 1996): "…Yes, I would accept the Bill Williams Fork locality at face value. Evidently Stahnke borrowed the specimen from the Snow Entomological Museum (F. H. Snow = Francis Huntington Snow), University of Kansas Museum of Natural History, … specimen was probably collected on a 1903, entomological expedition out of the University of Kansas, on the Atchison, Topeka & Santa Fe Railroad which has a branch line "Bill Williams Fork" running through Williams, Coconino County, Arizona." Byron Alexander, Curator of the Snow Museum, had this to say about Bigelow's comments (pers. comm., August 1996): "… I see no obvious errors or inaccuracies in what you have said about F. H. Snow or the locality in Arizona. I am most familiar with his locality records for pinned specimens of bees. While they are often rather imprecise, I don't recall ever seriously questioning their accuracy." The specimen, a somewhat large adult male (carapace length = 9.9 mm), is smooth and quite dark in color (probably due to prolonged preservation); the interocular area of the carapace is smooth with scattered granulation on the extreme anterior edge; the chelal fingers, when closed, show a somewhat prominent gap; the digital (*D1*) carina is well-developed; metasomal segment V is quite slender, exhibiting a length/width ratio of 3.5; the chelal ventral trichobothria number 17/18. The combination of these characters imply that *A. p. pococki* is the closest species match, but if the locality data is correct, one would assume it is *A. phaiodactylus*, since it is found just north of this locality in extreme southern Utah; all known *A. p. pococki* are found in coastal California and Baja California. At this time, we identify this specimen as *A. p. pococki* and unless additional specimens are found in northern Arizona matching the characters described above, the locality data will have to be considered spurious.

San Geronimo, Oaxaca (AMNH). Of the three questionable *Anuroctonus* localities, this one from Oaxaca is the most intriguing. The specimens were collected by Alexander Petrunkevitch in 1909 during an American Museum expedition to Mexico. These scorpions were identified by Petrunkevitch as *Vaejovis cristimanus* Pocock. In another label, at an unknown time, they were identified as *Anuroctonus phaiodactylus* by Willis Gertsch. We discuss here two plausible explanations, out of several, for this apparent spurious locality data (assuming that *Anuroctonus* indeed does not occur in Oaxaca): the locality label was incorrect, possibly switching the town/country of two countries where Petrunkevitch had collected (a suggestion offered by Norman Platnick, pers. comm., June 1996); or that the specimens where inadvertently switched with specimens from another jar containing *Anuroctonus*. In support of the first explanation, there is a San Geronimo in Marin Co., California, but it places *Anuroctonus* approximately 100 miles north of its known range. Coincidentally, this explanation also provides us with yet another report of *Anuroctonus* from the Bay area of California (see Contra Costa Co. record above). The second possibility is that these specimens were switched at one time (a time that would predate Willis Gertsch's arrival at the American Museum, the very early 1930s). In defense of this possibility is the opinion that Petrunkevitch would have not mistakenly identified *Anuroctonus* as *Vaejovis*, that is the specimens originally studied by Petrunkevitch were indeed a *Vaejovis* species, perhaps even *V. cristimanus*. Pocock's 1902 tome (from *Biologia Centrali-Americana*) was available at that time, with keys and excellent illustrations, which included both species in question, *Anuroctonus* and *Vaejovis cristimanus*. These specimens, a large male and female, are consistent structurally with *A. p. pococki*

Table IV. Morphometrics (mm) of *Anuroctonus pococki bajae* ssp. nov.

	Ojos Negros, Baja California Norte	Ojos Negros, Baja California Norte	Meling Rch., Baja California Norte	Jasper Trail, ABDSP, California	Jasper Trail, ABDSP, California	Pinyon Mtn., ABDSP, California
	Male Type	Female	Male	Male	Male	Male
Total length	51.20	38.75	56.55	52.80	55.15	42.70
Carapace length	7.25	6.40	8.70	8.10	8.40	6.30
Mesosoma length	16.55	17.20	16.25	15.70	18.15	14.45
Metasoma length	20.15	15.15	23.20	21.25	21.25	16.15
Metasomal segment I						
length	2.40	1.75	2.70	2.50	2.60	1.90
width	3.10	2.45	3.55	3.55	3.25	2.50
Metasomal segment II						
length	3.00	2.15	3.55	3.15	3.15	2.30
width	2.85	2.20	3.25	3.15	3.05	2.30
Metasomal segment III						
length	3.65	2.85	4.20	4.00	4.00	2.95
width	2.65	2.05	3.00	3.05	2.95	2.25
Metasomal segment IV						
length	4.50	3.50	5.25	4.70	4.70	3.65
width	2.50	2.00	2.85	2.85	2.85	2.10
Metasomal segment V						
length	6.60	4.90	7.50	6.90	6.80	5.35
width	2.10	1.80	2.30	2.30	2.30	1.75
Telson length	7.25	4.80	8.40	7.75	7.35	5.80
width	3.00	1.70	3.55	3.35	3.15	2.40
depth	3.15	1.55	3.55	3.25	3.15	2.35
Pedipalp length	23.95	17.60	27.65	25.45	25.25	20.15
Femur length	5.35	3.80	6.20	5.55	5.45	4.50
width	2.30	1.70	2.60	2.40	2.30	1.90
Patella length	5.95	4.50	7.00	6.50	6.30	5.15
width	3.25	2.50	3.65	3.35	3.15	2.70
Chela length	12.65	9.30	14.45	13.40	13.50	10.50
Palm width	3.95	3.00	4.50	4.40	4.20	3.25
depth	5.15	3.70	5.45	5.45	5.25	4.25
Movable finger length	7.30	5.50	8.70	7.75	7.85	6.10

Anuroctonus pococki bajae Soleglad & Fet, ssp. nov. (Figs. 5, 8–11, 13, 15, 20, 24, 30, 36, 39–40, 44–45; Table IV)

Holotype: male, 7 mi. E. Ojos Negros, Baja California Norte, Mexico; collectors S. C. Williams and V. Lee, 10 July 1969 (CAS). **Paratypes:** 7 mi. E. Ojos Negros (3,500 ft asl), Baja California Norte, Mexico, 10 July 1969 (Williams, Lee), 4 males and 1 female (CAS).

Diagnosis. Small to medium sized scorpion, carapace length of sexually mature males ranging 6.00–8.80 (7.544) (±0.609) [n = 81]. Light yellow to brown in overall color, chelal fingers dark brown to black. Dorsal surface of carapace and mesosoma exhibiting medium to heavy granulation. Ventral trichobothria of pedipalp chelae number 16–18 (17) (plus-minus standard error range and mean); digital carina (*D1*) of chelae well developed but not pigmented; interocular area of male carapace granulose; metasoma slender, segment V length/width ratio 2.98–3.23 (3.10) and metasoma length/carapace length ratio 2.53–2.70 (2.62) for male (plus-minus standard error range and mean); ventroexternal carina (*V1*) of chelae pitted to distinctly granulated.

Distribution. USA (extreme southern, inland California, south of the Sierra Nevada and east of the Cuyamaca and Laguna Mountains; Mexico (inland Baja California Norte, Sierra de Juárez and Sierra San Pedro Mártir, north of the Sierra de San Borja) (see map in Fig. 31).

Etymology. This scorpion subspecies is named after Baja California, Mexico, from where the type specimen originates.

Male. Description based on holotype male. Measurements of type specimen and other material are presented in Table IV. See Fig. 36 for a dorsal view of the male holotype.

Coloration. Carapace, legs, metasoma, pedipalps, and chelicerae yellow, tubercles and extreme anterior edge of carapace dark brown yellow; mesosoma, ventral aspect of metasomal segment V, and cheliceral fingers with brown fuscous patterns; pedipalpal fingers dark brown, digital carinae not pigmented.

Carapace. Anterior edge with subtle indentation; wide, deep indentation bisecting interocular area which is covered with large granules. Lateral eyes number four, small fourth eye positioned above most posterior eye. Median eye tubercle thin, positioned anterior of middle with the following length and width formulas: 310|725 and 95|575, respectively.

Mesosoma. Tergites I–VI smooth to rough at 10x; tergite VII covered with coarse granules, obscuring median and lateral median carinae. Sternites smooth; ventral lateral and median carinae very well developed on sternite V, broadly crenulate and highly tapered in an anterior to posterior direction, corresponding to same well developed carinae exhibited in metasomal segments I–III. Stigmata of medium length, thin oval-shaped.

Metasoma. Segments I–IV: dorsal and dorsal lateral carinae granulated to crenulate; lateral carinae granulated on basal 60 % of I, proximal 20 % of II, and essentially obsolete on III–IV; ventral lateral and median carinae of I–III exaggerated, highly raised from segment and broadly crenulate, tapering in an anterior to posterior direction, as that described for the two carinal pairs on sternite V; ventral lateral and median weak, rough to granulated on IV. Segment V: dorsal lateral carinae granulated; lateral granulated for 50 % of anterior aspect; ventral lateral and median serrulate, median bifurcated posteriorly, exhibiting a Y-shaped pattern. Intercarinal areas smooth. Dorsal lateral carinae of segment IV terminate directly at articulation condyle, not flared; extreme dorsal posterior aspect of segment V is highly flared.

Telson. Vesicle highly inflated laterally, juncture with aculeus exhibiting a swollen "bulb", indicative of a sexually mature male. Vesicle surface smooth and shiny, basal dorsal aspect missing vesicular "tabs".

Pectines. Short wide segments exhibiting length|width formula 270|145. Sclerite construction simplistic, three anterior lamellae and three middle lamellae, the basal plate the largest, abutted to basal anterior lamella; fulcra of medium development. Teeth number 9/9. Sensory areas well developed along most of tooth inner length. Basal piece elongated, no indentation, length|width formula 240|75.

Genital Operculum. Sclerites separated for most of length; genital papillae present but do not extend beyond posterior edge of plates.

Sternum. Type 2, deep posterior emargination present, well defined convex lateral lobes, slightly wider than long, length|width formula 440|520.

Chelicerae. Appendages elongated, movable finger dorsal edge with two small subdistal (*sd*) denticles; movable edge with two small denticles on basal half; basal half with heavy setal brush, serrulae absent. Ventral distal denticle (*vd*) considerably longer than dorsal (*dd*) counterpart. Fixed finger with four denticles, median (*m*) and basal (*b*) denticles conjoined on common trunk.

Pedipalps. Heavy chelate species, little or no scalloping on chelal fingers, thus not exhibiting sexual dimorphism in this structure. **Femur:** Dorsal internal, external, and ventral internal carinae equipped with large serrulate granules; ventral external rounded and granulate. Dorsal surface granulated; ventral surface with line of granules; internal and external faces smooth. **Patella:** Internal carinae with large serrulate granules; dorsal external carina irregularly granulated; ventral external serrate; exteromedian obsolete. All surfaces smooth; internal surface with a large well developed DPS, VPS quite small, represented by a solitary granule. **Chelal carinae:** digital (*D1*) carina strong, smooth; subdigital (*D2*) represented basally by four granules; dorsosecondary (*D3*) rounded and weak; dorsomarginal (*D4*) and dorsointernal (*D5*) rounded, irregularly granulose, the latter somewhat weak; ventroexternal (*V1*) strong, equipped with conspicuous serrated pigmented granules (Fig. 44), curving distally towards midpoint between movable finger condyles (internal of trichobothrium Et_1); ventromedian (*V2*) weak and rounded; ventrointernal (*V3*) strong, irregularly granulated; external (*E*) strong and smooth. **Chelal finger dentition:** median denticle (MD) row groups aligned in straight line; 5/5 and 6/6 internal denticles (ID) and 6/6 and 7/7 outer denticles (OD) on fixed and movable fingers, respectively. Basal outer denticle of movable finger slightly enlarged. No accessory denticles. **Trichobothrial patterns** (Fig. 30)**:** Type C, neobothriotaxic (major additive) type *Ch3* on chela and patella. Femur: trichobothrium *d* located next to dorsoexternal carina and adjacent to *i*. Patella: 23 ventral trichobothria (16 ventral and 7 "wrap-around" on external surface), most proximal petite; *eb* = 7, *est* = 2, *em* = 8, *est* = 4, and *et* = 3. Chela: 18/19 ventral trichobothria.

Legs. Both pedal spurs present, tibial spurs absent. Tarsus (III) with single median row of 8 stout spinules on ventral surface, terminating distally with a single spinule pair.

Hemispermatophore. See Fig. 27 for structure typical in genus.

FEMALE. Sexual dimorphism as discussed for *A. phaiodactylus* is reflected in this subspecies. Pectinal tooth counts: male = 7–10 (8.55) (±0.84) [201]: {8–9}→ 0.098; female = 4–8 (6.13) (±0.79) [076]: {5–7}→ 0.129 (see Fig. 37).

SPECIMENS EXAMINED.

USA: California: ***Riverside County:*** ABDSP: Coyote Canyon Road, 7.5 mi. SE Anza (3,600), 10 September 1997 (Soleglad, Pinion), adult and 7 juvenile males, 7 juvenile females (MES); ***San Bernardino County:*** San Bernardino National Forest, 5.7 mi. SW Onyx Summit, 20 June 1971 (Haradon, Marks), 1 subadult and 1 adult male (CAS); San Bernardino National Forest, 3.5 mi. SW Onyx Summit, 20 June 1971 (Haradon, Marks), 2 females (CAS); 0.7 mi. E Wrightwood, Rte 2, 7 July 1972 (Haradon, Marks), 5 males, juvenile female (CAS); 0.9 mi. E Wrightwood, Rte 2, 6 July 1979 (Haradon), 4 males (CAS); N Yucca Valley, 14 May 1970 (Haradon, Levtcke), female (CAS); ***San Diego County:*** ABDSP: S-22, 1.1 mi. E of Ranchita/Park entry, 12 August 1996 (Soleglad), 12 males (MES); ABDSP: Jasper Trail, 2.9 mi. S S-22 (3,620 ft asl), 6 May 1997 (Soleglad), adult and 2 juvenile females (MES); ABDSP: Jasper Trail, 0.5 mi. S S-22 (3,690 ft asl), 24 July 1996 (Soleglad), 8 males, 1 juvenile female (MES); 1.5 km SW Hwys S2/78 (2,700 ft asl), 1 September 1992 (Lowe, Hébert), 5 males and 1 female (GL); 0.5 mi. W. Banner (2,500 ft asl), 1 September 1992 (Lowe, Hébert), male (GL); ABDSP: Pinyon Mountain Rd., 4.3 mi. E. Hwy S2, 18 March 1972 (Soleglad, Erickson), adult and juvenile females (MES); ABDSP: Pinyon Mountain Rd., 4.3 mi E. Hwy S2 (), 4 June 1997 (Soleglad), 6 juvenile males, 2 juvenile females

(MES); ABDSP: Pinyon Mountain Rd., 4.3 mi. E. Hwy S2, 7 April 1973 (Soleglad, Erickson), 1 adult and 2 juvenile females, 2 adult and 1 juvenile males (MES); ABDSP: Pinyon Mountain Rd., 6.2 mi. E. Hwy S2, 15 April 1972 (Soleglad, Erickson), 2 juvenile females (MES); ABDSP: Pacific Crest Trail off Chihuahua Rd., 11.1 mi. E. Hwy 79, 8 July 1997 (Soleglad), subadult male and 2 subadult females (MES); ABDSP: Pacific Crest Trail off Chihuahua Rd., 11.1 mi. E. Hwy 79, 27 August 1998 (Soleglad, Himmerich), 12 males; Bankhead Spring, 30 December 1988 (Stockwell), female (USNM); Bankhead Spring, 30–31 March 1988 (Stockwell, Brown), 5 adult and 4 subadult males, 7 adult and 2 subadult females (USNM); Horse Haven Cmp, McCain Valley Res., 4 mi. NE Boulevard, 30 March 1988 (Stockwell, Brown), 2 males (USNM); McCain Valley Res., 7 April 1988 (Stockwell, Brown), male (USNM); Mission Gorge, 15 February 1988 (Stockwell), female (USNM).

MEXICO: **Baja California Norte:** 4 mi. SE El Condor, 1 April 1988 (Stockwell), male (USNM); El Condor, 1 April 1988 (Stockwell), subadult male, 2 females (USNM); El Progreso (5,200 ft asl), 1 April 1969 (Williams), juvenile male, 1 juvenile, 1 subadult, and 1 adult female (CAS); 19 N. Rancho El Topo (4,800 ft asl), 16 July 1969 (Williams, Lee), 2 males (CAS); 12 mi. S. La Rumorosa (4,500), 9 October 1965 (LaPre, Lent), adult female (AMNH); 2 mi. SW La Rumorosa (4,300 ft asl), 1 April 1969 (Williams), 5 females, 4 adult and 1 juvenile males (CAS); 5 mi. SW La Rumorosa (4,500 ft asl), 1 April 1969 (Williams), 1 male and 2 juveniles (CAS); 10 mi. E. Meling Ranch (4,000 ft asl), 13 July 1969 (Williams, Lee), 4 males (CAS); 18 mi. E. Meling Ranch (6,500 ft asl), 13 July 1969 (Williams, Lee), 2 males (CAS); 7 mi. E. Meling Ranch (3,000 ft asl), 13 July 1969 (Williams, Lee), 2 males (CAS); Meling Ranch, 4 May 1961 (Gertsch, Roth), adult male (AMNH); 7 mi. E. Ojos Negros (3,500 ft asl), 10 July 1969 (Williams, Lee), 5 males and 1 female (CAS); Puerto Santo Tomás (25 ft asl), 11 July 1969 (Williams, Lee), 2 males (CAS); 29 mi. E. Tecate, 17 July 1969 (Williams, Lee), 2 adult and 1 juvenile males (CAS).

Anuroctonus pococki pococki x *A. p. bajae* intergrades

California: ***San Diego County:*** ABDSP: Laguna Mountains, Kwaaymii Point, 0.1 mi. off S1 (5,900 ft asl), 14 August 1996 (Soleglad, Scheller), male and female (MES); ABDSP: Laguna Mountains, extreme north edge of ABDSP, Hwy S1, 1 July 1997 (Soleglad, Pinion), 2 adult and 1 juvenile males (MES); Laguna Mtn., male (JB); ABDSP: Chariot Canyon, 4.3 mi. S. Banner (Hwy 78) (3,400 ft asl), 30 August 1997 (Soleglad, Pinion), 13 males, adult and juvenile females (MES).

Subspecies status: We have opted to assign subspecies status to the inland populations of *A. pococki* for the following reasons: statistically, we do not see a "clean" separation of the plus-minus standard error ranges of these two populations such as that exhibited between the species *A. pococki* and *A. phaiodactylus*. In particular, in the primary character (the number of ventral trichobothria of the chela) we see a 30 % overlap between the two populations. In addition, we have identified a population (21 specimens examined) of *A. pococki* from the Laguna Mountains (San Diego Co., California) that is intermediate statistically in the ventral trichobothria counts, their standard error range overlapping with that of the coastal and inland populations by as much as 65–67%. In the other two characters separating these two subspecies, we see the Laguna population is intermediate also in its development of the chelal *V1* carina, exhibiting a rough to pitted surface; the chelal digital (*D1*) carina, however, is darkly pigmented as that found in the coastal population. Finally, this Laguna population is located in an area that essentially separates the coastal and inland populations of *A. pococki*, thus it is intermediate geographically as well. Therefore, based on the Laguna population's geographic location and intergradation of key diagnostic characters, we consider this a hybrid population between two subspecies of *A. pococki*. Note, since the Laguna population complied with *A. p. pococki* as to the pigmented chelal *D1* carina, we have included this population with *A. p. pococki* in all statistical analysis presented herein.

Anuroctonus species and subspecies: statistical analysis

We present a series of histograms (Figs. 49–55) showing the statistical data representing the diagnostic characters proposed herein for separating the species and subspecies of the genus *Anuroctonus*. Each histogram is organized as follows: For species *A. phaiodactylus* and subspecies *A. p. bajae*, the data is broken down into two populations each, "Idaho + Utah" and "Nevada + California" for *A. phaiodactylus*, and "California" and "Baja California Norte" for *A. p. bajae*. Each species and subspecies in the upper portion of the histograms are depicted with *gray* bars. The two species, *A. phaiodactylus* and *A. pococki*, are contrasted in detail where plus-minus standard error range and variance analysis results are stated (*black* bars).

The three morphometric ratios presented in this study were based on several sets of measurements taken of select material, over 1500 separate measurements in all. Only sexually mature males were considered. A full set of measurements were collected for 50 specimens as follows: 22 *A. phaiodactylus*, 15 from "Idaho + Utah", and seven from "Nevada + California"; 20 *A. p. bajae*, 13 from "California", and 7 from "Baja California Norte"; and eight *A. p. pococki*. In addition, metasoma segment V length and width were measured on a total of 146 specimens, roughly split between *A. phaiodactylus* and *A. pococki*; and over 310 carapaces were measured, 177 and 135 for *A. phaiodactylus* and *A. pococki*, respectively. The latter set of measurements were collected, in part, to determine the relative size of sexually mature males across the species and subspecies (see discussion elsewhere in this paper).

Trichobothria—the chela: The ventral trichobothria found on the chela is the primary diagnostic character separating *A. phaiodactylus* and *A. pococki*. This trichobothria series is neobothriotaxic (classified as type *Ch3*, see Soleglad & Fet, 2003b: 50) and exhibits a considerable variability in its range, 12–26. In addition, this trichobothrial series extends onto the external basal aspect of the chelal palm, lining up with the *Eb* series (see Figs. 29 and 30). The histogram depicted in Fig. 49 presents the statistical distribution of the chelal ventral trichobothria for all species and subspecies of *Anuroctonus* based on over 900 samples representing the entire geographic range of the genus. The species *A. phaiodactylus* and *A. pococki* exhibit significant plus-minus standard error range separation, over 30 %, and a negligible *p-value* result from variance analysis, showing fractional magnitudes of 160. Within species *A. phaiodactylus* we see a slight decrease in ventral trichobothria numbers in the "Idaho + Utah" population; and in subspecies *A. p. bajae*, we see no separation between its two studied populations, exhibiting a 100% overlap. Subspecies *A. p. bajae* and *A. p. pococki* also show differences, *A. p. pococki* clearly having the largest ventral trichobothria counts, though their plus-minus standard error ranges overlap by 30 %. When comparing the "Nevada + California" population of *A. phaiodactylus* with *A. p. bajae*, we see only a 7.5 % overlap of the standard error ranges. In the discussion section, we investigate the loss of accessory trichobothria in the chelal ventral series presumably due to speciation and radiation.

Carapace granulation: The interocular area of the carapace in sexually mature males is essentially smooth and shiny in species *A. phaiodactylus* (Figs. 7, 34, 41–42), whereas in *A. pococki*, this surface is quite granulose (Figs. 8, 35–36, 38–40). We modeled this character with three states, as shown in the histogram depicted in Fig. 50: state-1 = interocular area is smooth; state-2 = interocular area smooth, rough to granulose on extreme anterior edge; and state-3 = interocular area with light to heavy granulation. The histogram in Fig. 50, based on 328 samples, shows significant plus-minus standard error range separation of over 85%. The variance analysis *p-value* is negligible, depicting a fractional magnitude of 102. Within the two populations of *A. phaiodactylus*, we see a slightly smoother carapace in the "Idaho + Utah" population, but both populations' standard error range overlap is considerable, 82.4 %. Within the two subspecies of *A. pococki*, we see complete overlap of the standard error range.

Chelal digital carina (D1) development: The digital carina (*D1*) of the pedipalp chela is quite reduced in species *A. phaiodactylus*, showing little profile when viewed distally from the fingers (Fig. 48). In species *A. pococki*, the digital carina is well developed (Fig. 47). This character is modeled with four states, as shown in the histogram in Fig. 51: state-1 = carina obsolete to weak; state-2 = carina weak to rounded; state-3 = carina strongly developed, with light to no pigmentation; and state-4 = carina strongly developed, conspicuously pigmented. The last two states which, in part, depict carinal pigmentation are used to contrast the two subspecies of *A. pococki*. The histogram shown in Fig. 51, based on 415 samples, exhibits a significant statistical separation between the two *Anuroctonus* species, a plus-minus standard error range separation exceeding 89 %, and a very small *p-value* result from variance analysis, showing a fractional magnitude of 135. Within the two populations of species *A. phaiodactylus*, we see the "Idaho + Utah" population with the most reduced digital carina but there is over 90 % standard error range overlap. For the two subspecies of *A. pococki*, we see that both have well developed digital carinae, but in *A. p. pococki* this carina is in general pigmented. We consider this a diagnostic character between these two subspecies.

Morphometric ratios: We calculated and compared all possible morphometric ratios between sexually mature males of species *A. phaiodactylus* and *A. pococki* (253 ratios in all, i.e., 23 morphometrics compared pairwise). This resulted in the isolation of four key morphometrics that dominated the ratio comparisons, two per species: (1) metasoma segment V width, *A. phaiodactylus*, dominated 23 out 23 comparisons (stated as 23/0); (2) metasoma segment V length, *A. pococki*, 23/0; (3) carapace length, *A. phaiodactylus*, 22/1; and (4) metasoma length, *A. pococki*, 21/2. One can correctly conclude from these four morphometrics that the metasomal segment V is wider in *A. phaiodactylus* and narrower in *A. pococki*; the carapace is longer in *A. phaiodactylus*; and the metasoma length is longer in *A. pococki*. Based on these four measurements, we constructed three ratios that provide excellent diagnostic characters separating these two species: (1) metasoma segment V length/width, (2) metasoma length/metasoma segment V width, and (3) metasoma length/carapace length. See Fet & Soleglad (2002: 4–5) for a detailed description of the technique used for isolating key morphometrics ratios.

Metasoma segment V (L/W): Fig. 52, based on 146 samples, shows the result of this morphometric ratio, illustrating the somewhat thicker metasoma segment V in *A. phaiodactylus* and the relatively longer segment in *A. pococki*. We see that the plus-minus standard error overlap is minimal at 2+ % and the variance analysis *p-value* is quite negligible exhibiting fractional magnitudes 23 fold. In *A. pococki*, the two subspecies show essentially no separation and this is true also for the two populations of subspecies *A. p. bajae*. This implies that the metasomal segment V is proportionally the same within the species. For *A. phaiodactylus*, we see that the "Idaho + Utah" population exhibits the most separation from *A. pococki*, the "Nevada + California" population somewhat intermediate between the two. This implies presumably that the thickening of metasoma segment V in *A. phaiodactylus* is dependent, in part, on species radiation.

Metasoma length/segment V width: Fig. 53, based on 49 samples, depicts the result of this ratio, illustrating the relatively longer metasoma in species *A. pococki* and the thicker metasoma segment V in *A. phaiodactylus*. We have already established the thinner and longer segment V on *A. pococki* and likewise thicker and shorter segment on *A. phaiodactylus*, this morphometric ratio further supports this result and, in addition, implies that the lengthening of the metasoma in *A. pococki* is not restricted to segment V. For this ratio we see plus-minus standard error range separation of 14 % and a negligible *p-value* between the two species. For species *A. phaiodactylus* we see essentially no difference between its two populations used in this analysis; for species *A. pococki*, we see that subspecies *A. p. pococki* is partially distinguishable from *A. p. bajae*, but exhibiting considerable overlap.

Metasoma length/carapace length: Figure 54, based on 50 samples, illustrates the relatively larger carapace found in species *A. phaiodactylus* as it is compared to the relatively longer metasoma of *A. pococki*. An over 10 % plus-minus standard error range separation is exhibited between these two species. The populations of *A. p. bajae* show zero separation, but *A. p. pococki* exhibits a somewhat longer carapace than its sister sub-

Table V. Statistical distribution of pedipalp *patella trichobothrial counts* for genus *Anuroctonus*. Chelal ventral trichobothria distribution is shown for comparison. Statistical data presented for species and subspecies includes minimum, maximum, mean, and number of samples. * Plus-minus standard error range overlap/separation and variance analysis *p-value* comparisons are provided for species *A. phaiodactylus* and *A. pococki*.

	A. phaiodactylus	***A. pococki***	***A. p. pococki***	***A. p. bajae***	**Plus-Minus Standard Error Overlap / Separation % ***	**Variance Analysis P-value ***
Patella						
Ventral & External – Total	33–44 (39.32) [050]	35–52 (41.67) [100]	37–52 (43.11) [053]	35–45 (40.04) [047]	overlap = 66.71%	3.73E-06
Ventral (excluding “wrap around” trichobothria)	10–17 (13.50) [050]	11–19 (13.97) [100]	11–19 (14.58) [053]	11–15 (13.28) [047]	overlap = 92.70%	7.60E-02
External (including “wrap around” trichobothria)	23–28 (25.82) [050]	24–34 (27.73) [100]	24–34 (28.57) [053]	24–30 (26.79) [047]	overlap = 51.22%	4.50E-09
Ventral “wrap around” trichobothria	2–5 (3.60) [020]	3–7 (4.80) [040]	4–7 (5.24) [021]	3–7 (4.32) [019]	overlap = 44.76%	7.45E-05
***et* series**	2–4 (3.10) [020]	2–5 (3.45) [040]	3–5 (3.67) [021]	2–5 (3.21) [019]	overlap = 90.73%	5.03E-02
***em* series**	2–4 (3.10) [040]	2–7 (3.82) [091]	2–7 (4.12) [048]	2–7 (3.49) [043]	overlap = 79.35%	1.01E-04
Chela						
Ventral	12–18 (14.401) [387]	14–26 (18.025) [530]	15–26 (19.233) [257]	14–20 (16.886) [273]	separation = 30.55%	5.20E-160

species, though not as exaggerated as in *A. phaiodactylus*.

Chelal ventroexternal (V1) carina: The structure of the ventroexternal (*V1*) carina of the pedipalp chela provides a diagnostic character for separating the two subspecies of *A. pococki*. This carina is quite smooth and shiny in *A. p. pococki* (Figs. 29, 43) whereas in *A. p. bajae*, the carina is rough and pitted to distinctly granulated (Figs. 30, 44–45). Species *A. phaiodactylus* also exhibits a irregularly granulated ventroexternal carina (Fig. 46). In the histogram shown in figure 55, this character is modeled with four states: state-1 = carina smooth and shiny; state-2 = carina rough to pitted; state-3 = pitted to granulated; and state-4 = distinctly granulate. As depicted in the histogram, based on 420 samples, we see that the two populations of species *A. phaiodactylus* overlap considerably, the “Idaho + Utah” population exhibiting a slightly more granulated carina. The two subspecies of *A. pococki* show differences in this character, exhibiting a modest 32% overlap of their standard error range and a somewhat small *p-value* result. Interestingly, in subspecies *A. p. bajae* we see the Baja California Norte population with by far the most granulated *V1* carina, as exemplified by the male type specimen shown in figure 44; this carina is conspicuous with its individually pigmented serrate granules.

Trichobothria—the patella: We also collected statistical data on the trichobothria of the pedipalp patella, analyzing 150 samples (roughly 50 samples per species and subspecies) for gross counts of the external and ventral aspects of the segment. In addition, using a smaller dataset of 20 samples per taxon, some of individual external series are further analyzed. Table V presents these data, contrasting it with the ventral trichobothria statistics of the chelae.

Consistent with the ventral trichobothrial statistics of the chelae, we see, in general, that *A. phaiodactylus* does have lower counts in all six categories depicted in Table V than species *A. pococki*; and, also consistent with the chelae, subspecies *A. p. pococki* has the highest trichobothria counts in these categories across the three taxa. However, the statistical differences exhibited are quite small—the plus-minus standard error range overlap between the two species is 45–93 %, clearly indicating that none of these categories are good diagnostic characters. In stark contrast, the plus-minus error range separation of over 30 % exhibited in the chelal trichobothria statistics between the two *Anuroctonus* species and the significantly small variance analysis *p*-value do indicate a solid diagnostic character. Except for the ventral trichobothria, *A. p. bajae*, exhibits slightly larger counts in these six categories than *A. phaiodactylus*, and, exhibiting smaller counts than *A. p. pococki*, so the trend that was discussed in detail above concerning chelal ventral trichobothria is also reflected in the patellar trichobothria data.

Table VI. Percentage of loss (%) of chelal ventral trichobothria in genus *Anuroctonus*. *Gray* depicts percentage of loss between contiguous geographic areas, presumably paths of species and subspecies radiation and speciation. Note, the southern area of *A. p. pococki* and the state of Nevada for *A. phaiodactylus* are excluded due to irregular and/or low sampling. See Fig. 56 for population breakdowns.

		A. pococki					***A. phaiodactylus***				
		Cent.	**North**	**East**	**Hybrid**	***A. p. bajae***	**Calif.**	**Utah-S**	**Utah-C**	**Utah-N**	**Idaho**
A. pococki	**Cent.**		7.50	8.78	12.13	16.41	25.41	28.01	29.19	29.36	30.82
	North			1.38	5.00	9.63	19.36	22.18	23.45	23.63	25.21
	East				3.67	8.36	18.23	21.09	22.38	22.56	24.16
	Hybrid					4.87	15.11	18.08	19.42	19.61	21.27
	A. p. bajae						10.77	13.89	15.30	15.50	17.24
A. phaiodactylus	**Calif.**							3.50	5.08	5.30	7.25
	Utah-S								1.64	1.87	3.89
	Utah-C									0.24	2.29
	Utah-N										2.06

Discussion

Accessory trichobothria variability

Anuroctonus. The geographic distribution of *Anuroctonus* as it relates to the number of ventral chelal trichobothria proves to be quite interesting. As stated above, the number of accessory trichobothria is variable, and in particular, those found on the ventral aspect of the chelal palm are considerably variable (compare trichobothria data of the patella to that of the chela in Table V). Though highly variable, these trichobothria numbers are not random, but instead show consistency within geographic partitions, thus providing us with an excellent diagnostic character for separating the species and subspecies of *Anuroctonus*, as was demonstrated above using significant statistical data. As a hypothesis based on this data and analysis presented below, we also suggest that these differences in chelal trichobothria counts are due to the *loss of accessory trichobothria* which accompanies both *speciation* and the *geographic radiation* within a species (from its hypothetical center of origin). Below we support this hypothesis in detail by presenting data in particular for the genus *Anuroctonus* (Chactidae). To show that this hypothesis has legitimacy in other scorpion groups, we present data also for multiple species of *Hadrurus* (Caraboctonidae, superfamily Iuroidea) and *Euscorpius* (Euscorpiidae). It must be noted here that a corollary results from our hypothesis of accessory trichobothria *loss* (i.e., not *gain*)—that for any group of closely related taxa exhibiting variable neobothriotaxy on a particular pedipalpal segment surface, the taxon with *the largest* number of accessory trichobothria on this surface is presumably *the most primitive* member of that group.

In Fig. 56 we show the distribution of *Anuroctonus* species and subspecies broken down into contiguous geographic areas. Each area is indicated with the number (mean value) of ventral trichobothria found on the chela associated with that area and is colored with a shade of gray that is relative to this mean value. That is, we have a mean value range from 13.975 (i.e., *A. phaiodactylus*, Idaho) to 20.200 (i.e., *A. p. pococki*, central coastal California), and have mapped each area accordingly across 256 shades of gray where 13.975 is mapped to the high end, 255 (= white), and 20.200 is mapped to the low end, 0 (= black). Therefore, the relative difference of trichobothria numbers is indicated visually by the area's proportional shade of gray as well as by the specified mean value.

For subspecies *A. p. pococki* we have divided its geographic range into four areas: *central*, which includes California counties Los Angeles, Orange, western Riverside, and western San Diego; *northern*, which includes counties Monterey, San Benito, San Luis Obispo, Santa Barbara, and Ventura; *eastern*, which includes western Tulare, western Kern, western Riverside, and eastern San Diego counties; and *southern*, which includes extreme northern coastal Baja California Norte. The range of the species *A. phaiodactylus* is divided into six areas: California, Nevada, Idaho, and Utah; Utah is divided further into three areas: *south*, which includes counties Beaver, Washington, and Iron; *central*, which includes Utah and Milliard counties; and *north*, which includes counties Box Elder and Tooele. For those areas where we have reasonable sampling (only the state of Nevada, 38 samples, and the southern range of *A. p. pococki*, 4 samples, are represented with marginal number of samples), we see a definite geographic variation pattern in the numbers of ventral trichobothria of the chela. For example, the extreme coastal central area of *A. p. pococki* has the highest number of ventral trichobothria on the chela for any species or subspecies examined in this study, exhibiting 18.374–22.026 (20.200) [105] (i.e., plus-minus standard error range, mean, and number of samples), with some specimens exceeding counts of 24. In stark contrast, we see the Idaho population of *A. phaiodactylus* with a 12.988–14.962 (13.975) [081] statistical value set, lowest of all *Anuroctonus* populations, exhibiting a 30.82 % difference between these two diverse populations.

In Table VI we show the percentage of trichobothria loss between all populations of the three species and subspecies of *Anuroctonus* (only the Baja California area of *A. p. pococki* and Nevada of *A. phaiodactylus* are excluded due to uneven and/or minimal sampling). By closely examining the map in Fig. 56 and using Table VI as a reference, we can see that as *A. p. pococki* radiates from the coastal central area in northern, eastern, and southern directions, the number of accessory trichobothria reduces in each area accordingly, exhibiting a percentage of loss of 5.94–8.78 %. For species *A. phaiodactylus*, we also see a consistent loss of chelal trichobothria, radiating from California, thru Nevada and Utah, terminating in extreme southern Idaho, presumably the area most recently invaded by the genus *Anuroctonus* (Robert Anderson informed us that *Anuroctonus* has not been found north of the original locality reported in his paper on the scorpions of Idaho (Anderson, 1975); pers. comm., December 1996). For this species, we see less accessory trichobothria loss than that seen in *A. p. pococki*, ranging 3.50–7.25 %, the latter percentage representing considerable geographic distance (from California to Idaho). Also of interest is the comparison of trichobothria loss between the eastern population of *A. p. pococki*, the hybrid population, and subspecies *A. p. bajae*: we see 3.67 % and 4.87 % between the three, essentially dividing the percentage of loss between the two subspecies of 8.36 %.

Based on the consistency of accessory trichobothria loss evident in Fig. 56 as it relates to geographic direction, it is clear that we see a loss of accessory trichobothria during the radiation of a species as well as during speciation within the genus. We hypothesize here that this is due to the probable vestigial nature of accessory trichobothria. It is clear that neobothriotaxy in general has occurred several times in extant scorpions, but certainly well after the establishment of the fundamental orthobothriotaxic patterns that essentially delineate the four parvorders of Recent scorpions—whose origin undoubtedly occurred somewhere within the Permian and Triassic periods (290 to 206 Mya) (see Soleglad & Fet, 2003b: 121). The earliest known documented example of neobothriotaxy is that of *Palaeoeuscorpius* Lourenço (Lourenço, 2003), estimated at ca. 100 Mya (fam. Palaeoeuscorpiidae; found in the Cretaceous amber from France). Other evidence to support the vestigial nature of accessory trichobothria is that petite accessory trichobothria sometimes occur in cases where trichobothria loss is evident (see following discussion on *Hadrurus* and *Euscorpius*).

Other scorpion groups: Significant accessory trichobothria data have been gathered for the genera *Hadrurus* Thorell, 1876 (family Caraboctonidae) (Soleglad, 1976; Fet *et al.*, 2001, 2004) and *Euscorpius* Thorell, 1876 (family Euscorpiidae) (Gantenbein *et al.*, 2001, 2002; Fet & Soleglad, 2002, in press; Fet *et al.*, 2003). These data, as was the case for genus *Anuroctonus* discussed above, also suggest a consistent change in the number of accessory trichobothria as a species geographically radiates.

Genus *Hadrurus*: Table VII shows a statistical summary of the internal accessory and ventral trichobothria occurring on the chela of *Hadrurus*. In the species *Hadrurus arizonensis*, where the numbers of these two trichobothrial series are quite large, we see significant and *consistent* differences in the number of ventral trichobothria of the chela based on populations throughout western United States, Baja California, and Sonora, Mexico. Populations from northern Sonora exhibit the largest numbers in both series, and, moving from east to west direction, we see that populations from northern Baja California Norte, and extreme southern California, ABDSP being the most western edge, to Picacho on the Colorado River, exhibit the second largest numbers. Now moving northward in California to Riverside County, as well as into central Arizona, we see that trichobothria reduce in number, showing a percentage of reduction from the northern Sonoran population of 11.05/6.48 % (internal/ventral) and 7.40/4.01 % for Riverside and Arizona, respectively. The most southern population of *H. a. arizonensis* is found in Guaymas, Sonora, exhibiting double digit percentage drops in trichobothria, 18.16/11.17 %. The subspecies *H. a. austrinus*, which represents the most southern range of *H. arizonensis* in Baja California Norte, also exhibits a considerable drop in trichobothria number in these two series, with 19.94/8.86 %. It is interesting to point out that the percentage drop in accessory trichobothria number is more significant in the internal series than in the ventral series across all these observations. This is surprising since the number of accessory trichobothria in the internal series is much smaller in *Hadrurus*, 2–6 internal (across all six species) versus 11–22 ventral. This fact implies that the stability of the internal series is much more vulnerable to species radiation than in the ventral series. Two other conditions support this observation: (1) the accessory trichobothria in the internal series are in general petite in size, especially the more basal trichobothria, implying trichobothria that are in the process of being lost, a suggestion originally proposed by Soleglad & Fet (2001: Appendix A); and (2) internal accessory trichobothria are absent altogether in *Hadrurus*'s sister genus *Hoffmannihadrurus* Fet & Soleglad, hypothesized to be a recent derivation (see Fet *et al.*, 2004)

In *Hadrurus*'s "*spadix* complex" (see Fet *et al.*, 2001), we see a reduction in the internal trichobothrial series of the chela from species *H. obscurus* to *H. spadix*, exhibiting 27.60 % drop in trichobothria (i.e., from three accessory trichobothria to two). The differences in the number of ventral trichobothria between these two closely related species is essentially nil, ex-

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Table VII. Chelal trichobothria statistics of genus *Hadrurus*, depicting internal accessory and ventral trichobothria (*H. pinteri* not shown). Data includes plus-minus standard error range, mean, and number of samples. *All population references for *H. concolor* and *H. hirsutus* occur in Baja California Sur, Mexico.

	Internal Accessory Trichobothria (n = 594)	**Ventral Trichobothria (n = 576)**
	***Hadrurus arizonensis arizonensis* (n = 211/209)**	
Northern Sonora	(5.537–6.376)(5.957)[046]	(18.902-20.780)(19.841)[044]
ABDSP, Calif.	(5.196-6.233)(5.714)[035]	(17.940-20.338)(19.139)[036]
Picacho, Calif.	(5.236-6.176)(5.706)[017]	(17.846-21.095)(19.471)[017]
Northern Baja Norte	(5.064-6.079)(5.571)[021]	(18.663-20.290)(19.476)[021]
Central Arizona	(4.954-6.077)(5.515)[066]	(18.078-20.013)(19.045)[066]
Riverside, Calif.	(4.817-5.783)(5.300)[010]	(17.542-19.569)(18.556)[009]
Guaymas, Sonora	(4.533-5.217)(4.875)[016]	(16.668-18.582)(17.625)[016]
	***Hadrurus arizonensis austrinus* (n = 26/24)**	
Baja Norte	(4.340-5.199)(4.769)[026]	(16.801-19.366)(18.083)[024]
	***Hadrurus obscurus* (n = 52/45)**	
Southwest USA	(2.657-3.343)(3.000)[052]	(13.986-15.836)(14.911)[045]
	Hadrurus spadix* (n = 116/112*)	
Southwest USA	(1.793-2.552)(2.172)[116]	(14.250-15.857)(15.054)[112]
	***Hadrurus concolor* (n = 155/151)**	
Los Bombas*	(3.543-4.372)(3.957)[047]	(15.962-18.169)(17.065)[046]
San Ignacio*	(3.615-4.203)(3.909)[022]	(16.471-18.892)(17.682)[022]
Santa Rosalia*	(3.822-4.723)(4.273)[044]	(17.821-19.560)(18.690)[042]
Cuidad Constitucion*	(3.799-4.868)(4.333)[036]	(16.995-18.834)(17.914)[035]
Los Aripes*	(4.150-5.183)(4.667)[006]	(16.663-18.337)(17.500)[006]
	***Hadrurus hirsutus* (n = 27/28)**	
Cabo San Lucas*	(3.845-4.229)(4.037)[027]	(15.165-16.335)(15.750)[028]

hibiting less than 1 % difference. We suggest here that the reduction of internal accessory trichobothria number shown in *H. spadix* is a derivation of this species, thus a product of speciation. This suggestion is further supported by the extensive geographic radiation seen in *H. spadix*, which is found as far north as the states of Idaho and Oregon, whereas *H. obscurus* is restricted to southern and central California, occurring sympatrically in ABDSP with *H. a. arizonensis*. Reduction in chelal trichobothria between the two species complexes exhibits significant differences of 55.90/21.21 %, the "*arizonensis* complex" with the larger numbers. Since these two complexes combined form a monophyletic clade (as demonstrated by Fet *et al.*, 2001), we can expand our hypothesis of speciation and radiation even further, to a higher taxonomic level. We suggest that the reduction of accessory trichobothria in the "*spadix* complex" lineage is a synapomorphy for that complex, implying that this complex is the most recently derived.

In the "*hirsutus* complex" we see similar consistent reduction in the ventral chelal trichobothria for species *H. concolor*: the Santa Rosalia (Baja California Sur) population exhibits the largest ventral trichobothrial count, which reduces in number in populations both in a northern and southern direction from Santa Rosalia. Specimens from the more northern Los Bombas exhibited a 8.69 % reduction in ventral trichobothria, and those from the more southern Los Aripes, showed a 6.36 % reduction. The slight differences in internal trichobothria number for these five populations did not demonstrate any consistent trend, exhibiting differences of 1.21 % to 8.52 % between adjacent populations. For species *H. concolor* and *H. hirsutus*, we see drops in the latter for both the internal and ventral chelal trichobothria series, exhibiting 2.82/11.54 % difference. The significant lost of ventral trichobothria is considered a derivation of *H. hirsutus*, whose range is somewhat restricted to the Cape region.

For genus *Hoffmannihadrurus* Fet & Soleglad, 2004 (two species of which are found in southern Mexico; see Fet *et al.*, 2004), we see a drastic difference in the number of ventral trichobothria between *H. gertschi* and *H. aztecus*, exhibiting a 18.52 % drop in the latter. This difference, however, may not be due to the recent speciation event since these two species are quite distinct in other aspects. Common to both, and a synapomorphy for the genus, is the absence of internal accessory trichobothria. However, *H. gertschi* has 3–4 external accessory trichobothria on the chelal palm which are absent in *H. aztecus*.

Genus *Euscorpius*: Large numbers of *Euscorpius* specimens have been examined by our research group (Fet, 1993, 2000; Fet *et al.*, 2003; Fet & Soleglad, 2002; Gantenbein *et al.*, 2001, 2002) as well as by previous workers (Caporiacco, 1950; Kinzelbach, 1975; Valle, 1975; Vachon & Jacques, 1977; Bonacina, 1980; Scherabon, 1987). In particular, statistics involving the pedipalp trichobothria is commonly collected and published. In our ongoing research efforts of this interesting scorpion genus, we have tabulated an extensive database based on specimens examined by us as well as from published records from other researchers. Presently, our database includes well over 6500 samples of each major trichobothrial series of *Euscorpius*, spanning all known species. In addition, these data are carefully organized into applicable populations on a species by species basis.

Table VIII. Patellar trichobothria statistics of select species of genus *Euscorpius*. [1]Islands off southeastern Spain (data from Gantenbein et al., 2001). [2]Original subspecies of Caporiacco distributed throughout Italy, Slovenia, and Croatia, now considered *E. tergestinus* (data from Fet & Soleglad, 2002). The two populations labeled as *E. c. tergestinus* represent the type locality (near Trieste, Italy) and Slovenia/Croatia, respectively. Note, populations from France, *E. c. niciensis*, and Corsica, *E. c. corsicanus*, are excluded from this table. Some of the included populations ("*E. c. concinnus*") also could represent a different, cryptic species (Vignoli *et al*., 2004, pers. comm.). [3]Original subspecies of Caporiacco now considered members of *E. sicanus* (data from Fet et al., 2003). *E. c. 'mesotrichus'* are populations from Greece and *E. c. canestrinii* represents a population from the island of Sardinia

	Patellar *et* Trichobothria	Patellar Ventral Trichobothria
***Euscorpius balearicus*[1]**		
Mallorca	(7.388-9.052) (8.220) [59]	(11.137-13.120) (12.129) [70]
Menorca	(6.902-7.932) (7.417) [12}	(9.777-10.556) (10.167) [12]
Cabrera	(6.309-7.191) (6.750) [28]	(9.557-10.505) (10.031) [32]
Cabrera Islets	(6.040-7.047) (6.543) [46]	(9.496-10.631) (10.064) [47]
***Euscorpius tergestinus*[2]**		
E. c. oglasae	(4.786-5.522) (5.154) [26]	(6.690-7.925) (7.308) [26]
E. c. concinnus	(5.651-6.296) (5.973) [412]	(7.567-8.477) (8.022) [411]
E. c. apuanus	(5.693-6.476) (6.084) [107]	(7.729-8.813) (8.271) [107]
E. c. picenus	(6.023-7.234) (6.628) [78]	(8.100-9.208) (8.654) [78]
E. c. aquilejensis	(5.662-6.374) (6.018) [56]	(8.334-9.416) (8.875) [56]
E. c. tergestinus	(5.829-7.396) (6.612) [129]	(8.682-10.264) (9.473) [129]
E. c. tergestinus	(6.542-8.085) (7.313) [249]	(9.406-11.055) (10.230) [256]
***Euscorpius sicanus*[3]**		
E. c. calabriae	(4.690-5.925) (5.308) [26]	(6.756-8.168) (7.462) [26]
E. c. palmarolae	(4.596-6.547) (5.571) [7]	(9.000-9.000) (9.000) [7]
E. c. sicanus	(4.948-6.316) (5.632) [19]	(8.001-9.181) (8.591) [22]
E. c. ilvanus	(5.795-6.597) (6.196) [46]	(8.253-9.443) (8.848) [46]
E. c. argentarii	(6.209-7.166) (6.688) [16]	(9.085-10.290) (9.688) [16]
E. c. garganicus	(6.320-7.188) (6.754) [65]	(9.098-10.447) (9.773) [66]
E. c. 'mesotrichus'	(6.511-7.776) (7.144) [153]	(9.379-11.029) (10.204) [152]
E. c. canestrinii	(7.200-8.355) (7.778) [27]	(10-472-11.735) (11.103) [184]

Table VIII presents statistics of the patellar external *et* and ventral series of trichobothria for three *Euscorpius* species. *E. balearicus* (see Gantenbein *et al.*, 2001) is isolated on the Balearic Islands off the coast of southeastern Spain. The drop in number of trichobothria in both of these series is dramatic in this isolated species: from the largest island, Mallorca, we see drops in both series of 9.77/16.17 % in the smaller island of Menorca, and even a larger reduction in the quite small Cabrera Island, 17.88/17.30 %. In the *et* series we even see a drop from Cabrera to the adjacent tiny islets, 3.07 %. In this example, species radiation (through either vicariance or dispersal) could be caused by the existence of additional smaller islands based around Mallorca, in each case the number of accessory trichobothria being reduced.

Fet & Soleglad (2002: 16–24, Fig. 34) showed the reduction of the external *et* and ventral trichobothrial series of species *E. tergestinus*: it is clear that the number of accessory trichobothria series reduces in number from Slovenia and Croatia (Dalmatian coast) to northwestern Italy. In our Table VIII, we see consistent drops in accessory ventral trichobothria, contiguous geographic areas losing from 2.49 % to 8.90 %, total reduction from the Slovenia/Croatia population to the Tuscany, Italy population is 28.56 %. We see comparable reductions in the *et* series, from Slovenia/Croatia to Tuscany, Italy, 29.52 %. For this series the population from Abruzzo, Italy showed higher counts than its adjacent eastern population, exhibiting some inconsistency with this trend.

Fet *et al.* (2003) presented detailed trichobothria statistics for the species *E. sicanus*, whose distribution spans from Greece in the east to Sardinia and Tuscany, Italy, in the northwest, and to Sicily and Malta, in the southwest. For this species, which exhibits a somewhat complicated geographic distribution, we see trends of trichobothria loss in segments of this somewhat disjunct distribution: from northern to southern Italy, especially in Sicily and south to Malta, we see drops in the two trichobothria series of 16.61/12.09 %. Isolated populations found in Greece and Sardinia exhibited the largest counts in these two trichobothria series, differing by 27.59/22.62 % from the Sicily and Malta populations. Our independent DNA phylogeny (Fet *et al.*, 2003) demonstrated that the Maltese population is indeed closest to the Sicilian *E. sicanus*; the Maltese Islands were connected to Sicily in Late Miocene (Messinian) times, and may have been connected again during Pleistocene sea-level lows (Schembri, 1992; Hunt & Schembri, 1999). It appears therefore that the earlier divergence and radiation of *E. sicanus* across its currently fragmented range could reflect early Tertiary biogeographic events.

The apparent closest relative of *E. sicanus* is the Balkan species *E. hadzii*, which also shows large numbers of trichobothria in these two series, comparable to the Greece and Sardinian populations of *E. sicanus* (see Fet *et al.*, 2003: Fig. 6). These two species share the unique external *eb* series which exhibits an unique pattern of five trichobothria, but differ in the number of trichobothria in the eb_a series. If this apparent relationship is true, then we see the reduction of eb_a trichobothria in *E. sicanus* as a derivation caused by speciation. In species *E. hadzii*, we also see a reduction of the eb_a series across the species' range from Croatia and Serbia & Montenegro eastward to Bulgaria (Fet & Soleglad, in press), showing a 22.16 % drop in number. In this species, all variable patellar external series reduce in number as well in this same easterly direction to Bulgaria, exhibiting drops in trichobothria counts of 19.76 % for the ventral series, 10.05 % for the *et* series, and 18.40 % for the *em* series.

Gantenbein *et al.* (2002) elevated *E. naupliensis* (C. L. Koch, 1837) to species status showing it is a distinct but close relative of *E. italicus*. These two species form a distinct subgenus *Polytrichobothrius* Birula, 1917. *E. naupliensis* is isolated in the Greek Peloponnese and Zakynthos Island, essentially showing complete separation from *E. italicus* which is found from northern Greece and Albania to Italy and southern Switzerland. The primary character separating these two species is the obsolescence (or near obsolescence) of the unique esb_a series, found only in this species complex. In *E. italicus* this series (entirely composed of accessory trichobothria) can number from 5–11 (7–9) trichobothria; sometimes for the larger counts, one or two of these trichobothria are petite. For *E. naupliensis*, we see 0–2 (0–1) trichobothria in this series, the more southern populations in the Peloponnese having lost the esb_a series altogether (statistics based on 98 specimens). Again, we see a drastic drop in accessory trichobothria in this species, hypothesizing here a synapomorphy for *E. naupliensis* separating it from *E. italicus*. It remains to be seen if the unique accessory esb_a series in *E. italicus* exhibits finely tuned geographic variation; according to our recent pilot genetic study (Fet *et al.*, in press), this species may have radiated very recently from glacial refugia, and could present a "control study" of accessory trichobothria reduction trend at Pleistocene or even Holocene scale.

As a final comment for genus *Euscorpius*, it must be stressed that the Mediterranean area is highly complex, and therefore, any attempt to ascertain a species geographic radiation over large distances is quite difficult. Ecologically diverse, species of *Euscorpius* occupy a variety of habitats from the Mediterranean shoreline to the high altitudes of the Alps, Balkans, and Taurus. Numerous dispersal, vicariance, isolation, and extinction events could profoundly influence evolution and modern distribution of *Euscorpius* species. The Mediterranean Sea basin experienced complex biogeographic changes over the Cenozoic era, with sea level changes (including Miocene desiccation event; Hsü, 1972), which could have imposed biogeographic patterns such as detected by Oosterbroeck & Arntzen (1992) for the most ancient split between Iberian/Italian lineages versus younger, Asia Minor-Transmediterranean lineages.

Phylogenetic considerations

We conducted a simple cladistic analysis using PAUP* (Swofford, 1998) of the three species and subspecies of *Anuroctonus* in order to ascertain the specific character derivations of these taxa. An "all-zero outgroup" was established to represent the *de facto* primitive state of these somewhat localized species level characters. We opted not to use *Anuroctonus*'s sister genus *Uroctonus*, since the two genera are so distinct, and because many of the characters were not particularly applicable to *Uroctonus* as it related to the proposed speciation of *Anuroctonus*; in particular, the loss of accessory trichobothria on the chela (i.e., *Uroctonus* is orthobothriotaxic), morphometric ratios, granulation, and pigmentation, all clearly species level characters, accounting for more than half of the characters used in this analysis.

We created nine characters, most of which were discussed in the body of this paper as diagnostic for separating the three taxa (see Table IX). Without any assumptions, the analyses resulted in three equally parsimonious trees, reflecting all possible combinations of phylogeny between the three taxa. That is, none of the nine characters were informative. Based on our hypothesis of accessory trichobothria loss during speciation and the geographic radiation of a species, as clearly indicated from detailed statistical data and simple observation of geographical distribution, we decided to order character-1 which models the number of chelal ventral trichobothria to reflect this hypothesis: (0, (1, (3)), 2); 0 = orthobothriotaxic, primitive state; 1 = maximum neobothriotaxy, *A. p. pococki*; 2 = accessory trichobothria loss-1 (*A. phaiodactylus*); and 3 = accessory trichobothria loss-2 (*A. p. bajae*). Note that this ordering assumes that the species with the highest number of accessory trichobothria is primitive, and any other species or subspecies with a lower number of accessory trichobothria represents a derivation from this state. Although this is a very simplistic model of accessory trichobothria evolution, we believe that, with the limited number of species, their connected geographical ranges, and the detailed analysis of trichobothria loss as it relates to geographical distribution, nothing more complicated is required. With this character ordered, we resulted in a single tree reflecting our presumed phylogeny, with character-1 being the only informative character: ((*A. p. pococki*, (*A. p. bajae*)), *A. phaiodactylus*). Predictively, we have a perfect Hennigian condition, the CI and RI indices equal 1, thus a homoplasy index of zero. This means, assuming our ordered character correctly reflects the evolution of the species in this genus, that the resulting character distribution described below can be assumed as correct.

Character derivations. *A. phaiodactylus* is by far the most derived species of the genus, exhibiting no less than seven synapomorphies: reduction in accessory trichobothria (loss-1), severe reduction or obsolescence of the digital (*D1*) carina, significant reduction or absence of granulation on the carapace, the thickening of the metasoma (two morphometric ratios), the enlargement of the carapace, and allopatric speciation from its and *A. pococki*'s common ancestor. *A. p. bajae* exhibited two synapomorphies, the reduction in accessory trichobothria (loss-2) and the increased granulation of the chelal ventroexternal (*V1*) carina. *A. p. pococki* has two derivations, the darkening of the *D1* carina and the smoothing of the *V1* carina.

Table IX. Character data matrix for species and subspecies of genus *Anuroctonus* using an *all-zero* outgroup. Character 1 is *ordered* as follows: (0, (1, (3)), 2). See sections discussing statistical analysis for more detailed data on these character states.

Number	Description	States and Their Assignments
1	Chela ventral trichobthria	0 = Zero outgroup 1 = primitive *Anuroctonus* (*A. p. pococki*) 2 = reduction-1 (*A. phaiodactylus*) 3 = reduction-2 (*A. p. bajae*)
2	Digital (*D1*) carina development	0 = Zero outgroup 1 = well developed (codes 3-4, *A. p. pococki, A. p. bajae*) 2 = obsolete to weak (codes 1-2, *A. phaiodactylus*)
3	Digital (*D1*) carina pigmentation	0 = Zero outgroup 1 = non-pigmented (*A. p. baja, A. phaiodactylus*) 2 = pigmented (*A. p. pococki*)
4	Interocular area of carapace	0 = Zero outgroup 1 = granulated (code 3, *A. p. pococki, A. p. bajae*) 2 = non-granulated (codes 1-2, *A. phaiodactylus*)
5	Metasoma length/V width	0 = Zero outgroup 1 = metasoma long (*A. p. pococki, A. p. bajae*) 2 = metasoma short (*A. phaiodactylus*)
6	Metasoma V, length/width	0 = Zero outgroup 1 = segment thin (*A. p. pococki, A. p. bajae*) 2 = segment wide (*A. phaiodactylus*)
7	Metasoma length/carapace length	0 = Zero outgroup 1 = carapace short (*A. p. pococki, A. p. bajae*) 2 = carapace long (*A. phaiodactylus*)
8	Ventroexternal (*V1*) carina development	0 = Zero outgroup 1 = rough-granulated (*A. phaiodactylus*) 2 = pitted-distinctly granulated (*A. p. bajae*) 3 = smooth (*A. p. pococki*)
9	Geographic range	0 = Zero outgroup 1 = parapatric (*A. p. pococki, A. p. bajae*) 2 = allopatric (*A. phaiodactylus*)

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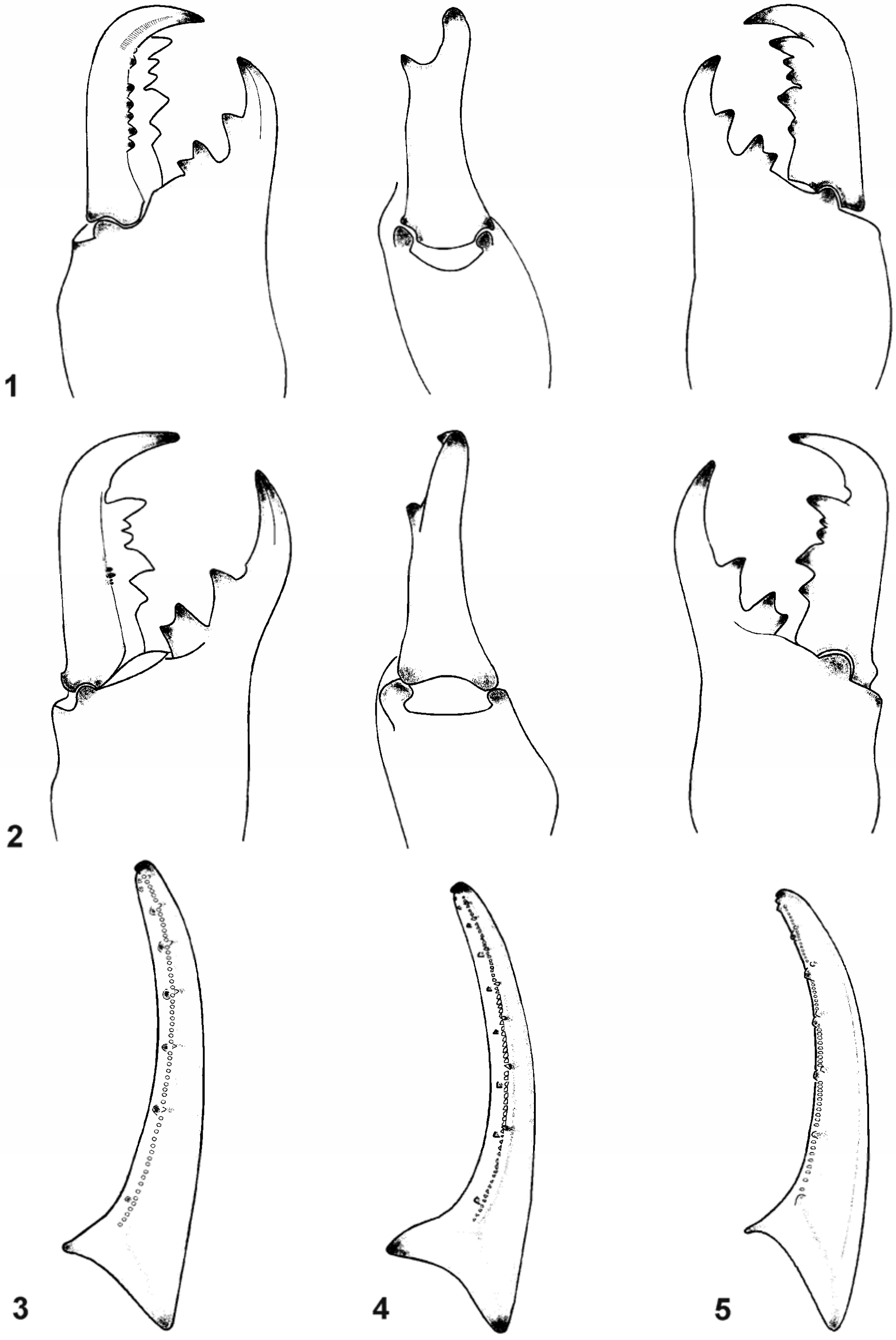
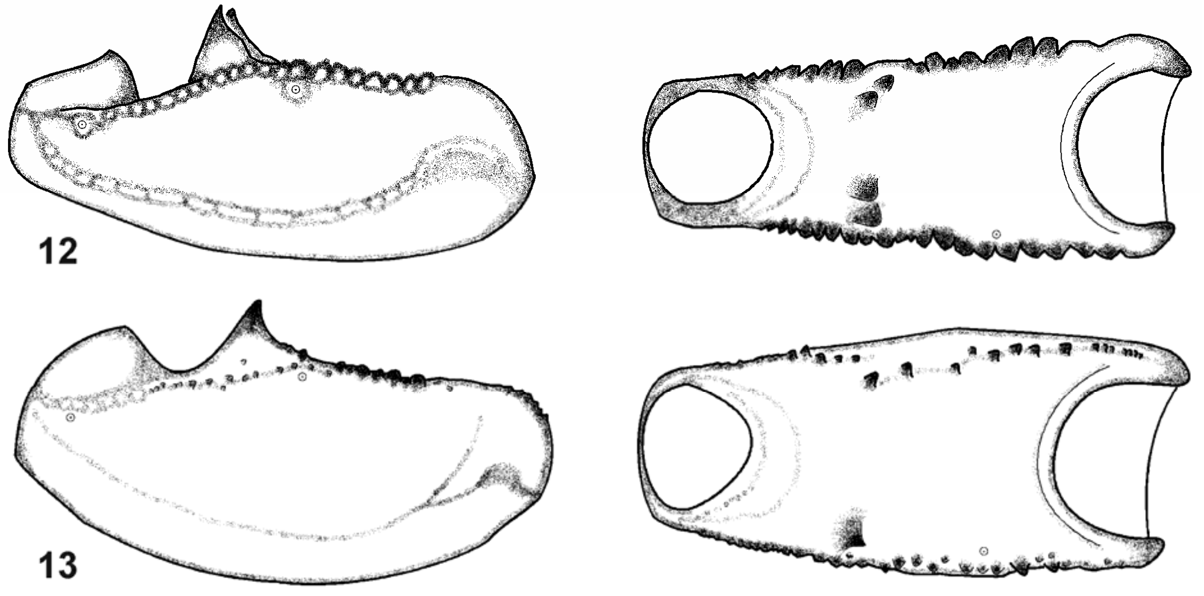


Figs. 1–5: 1 and **2.** Chelicerae, ventral (left), external (center), and dorsal (right) views. **3–5.** Pedipalp chelal finger dentition, movable finger. **1.** *Uroctonus mordax mordax*, male, Foresta, Yosemite National Park, Mariposa Co., California. **2.** *Anuroctonus phaiodactylus*, male, Garrison, Beaver Co., Utah. **3.** *Uroctonus mordax mordax*, Yosemite National Park, Mariposa Co., California, female. **4.** *U. m. pluridens*, male, Santa Clara, Santa Clara Co., California. **5.** *Anuroctonus pococki bajae*, male, Pinyon Mountains, ABDSP, San Diego Co., California.

Figs. 6–7: *Uroctonus* and *Anuroctonus*, carapace. **6.** *Uroctonus mordax mordax*, male, Alta Sierra, Sequoia National Park, Kern Co., California. **7.** *Anuroctonus phaiodactylus*, male, Grantsville, Tooele Co., Utah.

►

Figs. 8–11: *Anuroctonus pococki bajae*, male, Jasper Trail, ABDSP, San Diego Co., California. **8.** Lateral anterior view of carapace showing median and lateral eyes, right view. **9.** Lateral eyes, right view. **10.** Close-up of lateral eyes, right view, showing four eyes (numbered in *white*). **11.** Ventral edge of right cheliceral movable finger showing configuration of setae.



Figs. 12–13: Pedipalp patella showing carinae, Dorsal Patellar Spurs (DPS) and Ventral Patellar Spurs (VPS). Dorsal (left) and internal (right) views. **12.** *Uroctonus mordax mordax*., male, Foresta, Yosemite National Park, Mariposa Co., California. **13.** *Anuroctonus pococki bajae*, male, Chihuahua Road, ABDSP, San Diego Co., California.


8
20kU X15 1mm 444475


9
20kU X35 500μm 444475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20kU X100 100μm 444475


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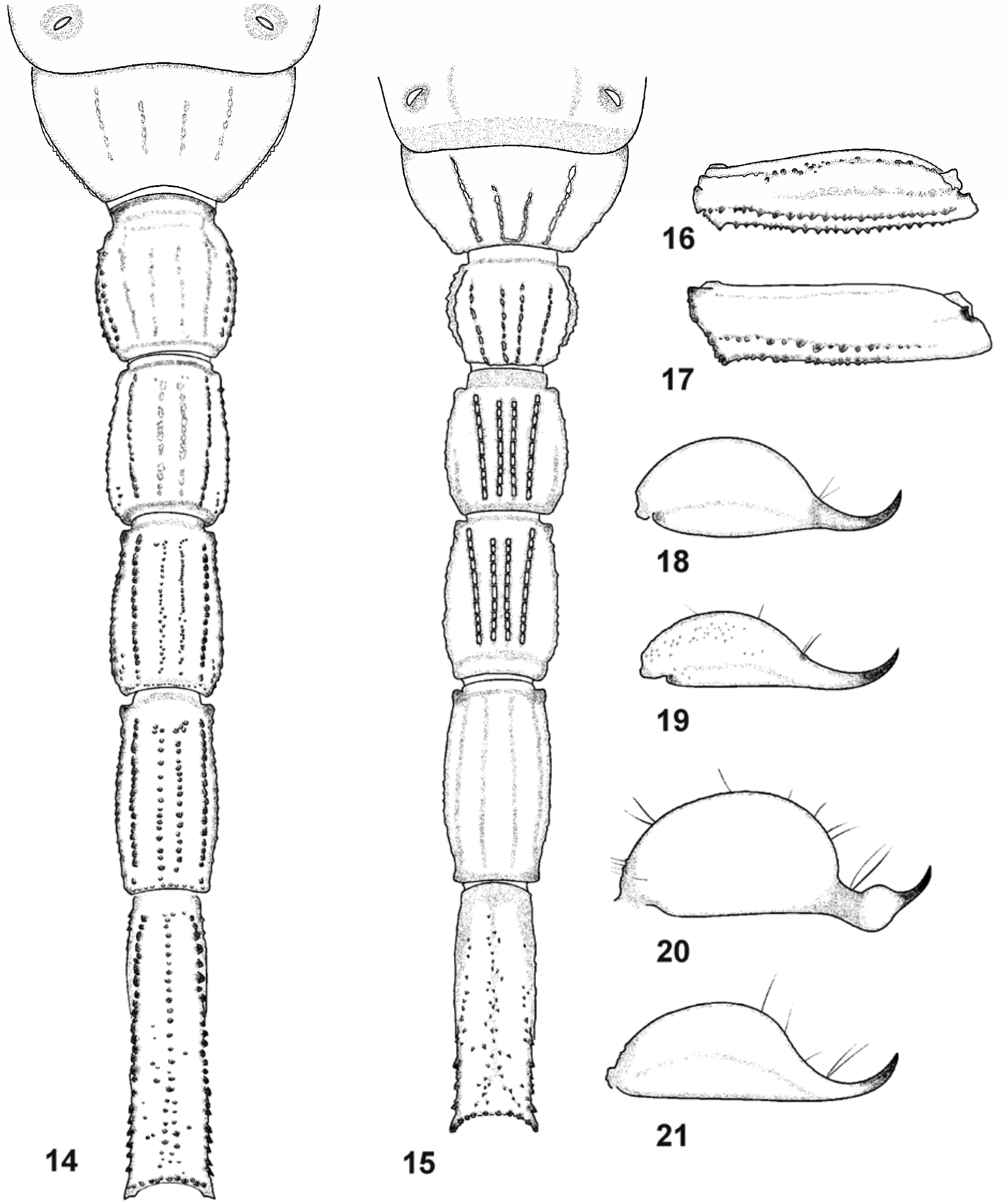
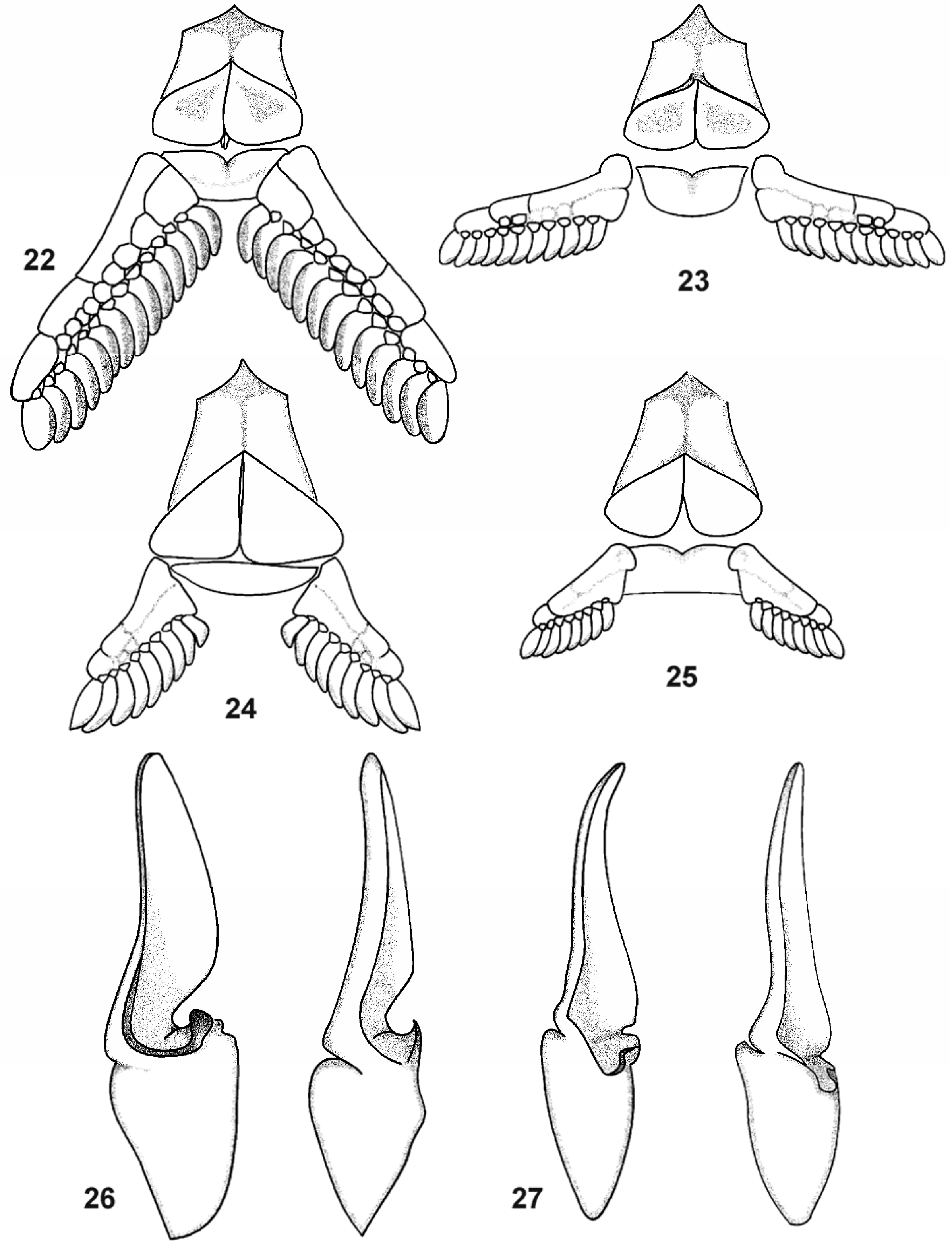


Figs. 14–21: 14–15. Metasoma and mesosoma (sternites IV–V), ventral view. **16–17.** Metasomal segment V, lateral view, showing the flared distal aspect of dorsal lateral carinae on *Anuroctonus* as compared to *Uroctonus*. **18–21.** Telson, lateral view. **14.** *Uroctonus mordax pluridens*, male, Santa Clara, Santa Clara Co., California. **15.** *Anuroctonus pococki bajae*, male, Pinyon Mountains, ABDSP, San Diego Co., California. **16.** *Uroctonus mordax mordax*, male, Foresta, Yosemite National Park, Mariposa Co., California. **17.** *Anuroctonus phaiodactylus*, male, Holbrook, Oneida Co., Idaho. **18.** *U. mordax mordax*, male, Lagunitas, Marin Co., California. **19.** *Uroctonus franckei*, female, June Lake, Mono Co., California. **20.** *A. pococki bajae*, male, Chihuahua Road, ABDSP, San Diego Co., California. **21.** *Anuroctonus p. pococki*, female, San Dimas Canyon, Los Angeles Co., California.



Figs. 22–27: 22–25. Sternum, genital operculum and pectines. **26–27.** Hemispermatophore, external (left) and ventroexternal (right) views. **22.** *Uroctonus franckei*, male, June Lake, Mono Co.,California. **23.** *U. mordax mordax*, female, Yosemite National Park, Mariposa Co., California. **24.** *Anuroctonus pococki bajae*, male, Chihuahua Road, ABDSP, San Diego Co., California. **25.** *A. p. pococki*, female, San Dimas Canyon, Los Angeles Co., California. **26.** *Uroctonus mordax mordax*, Weott, Humboldt Co., California. **27.** *Anuroctonus phaiodactylus*, Holbrook, Oneida Co., Idaho.

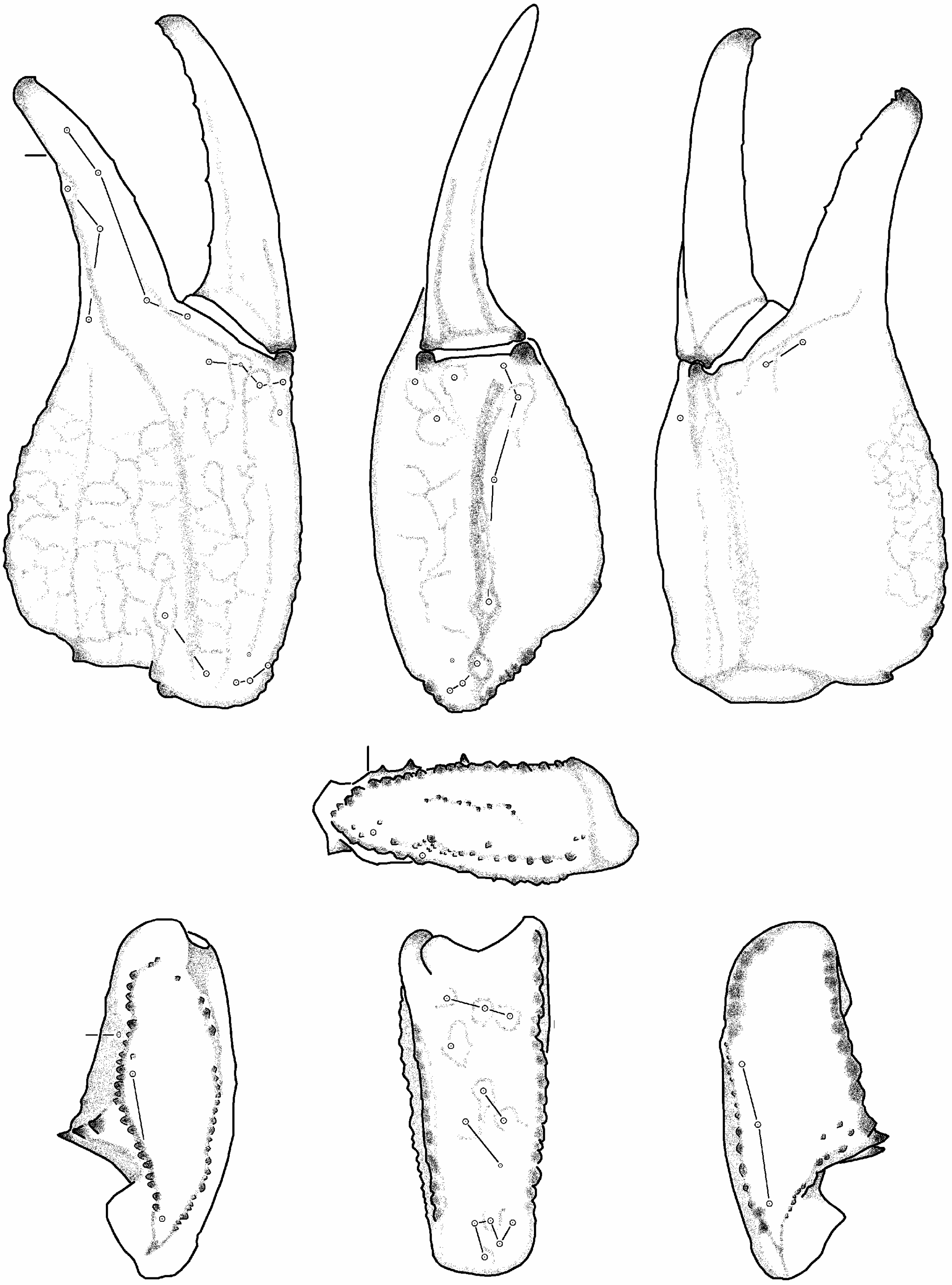


Fig. 28: Trichobothrial pattern of *Uroctonus m. mordax*, male, Foresta, Yosemite National Park, Mariposa Co., California. Chela (top), external, ventral and internal views. Femur (middle), dorsal view. Patella (bottom), dorsal, external and ventral views.

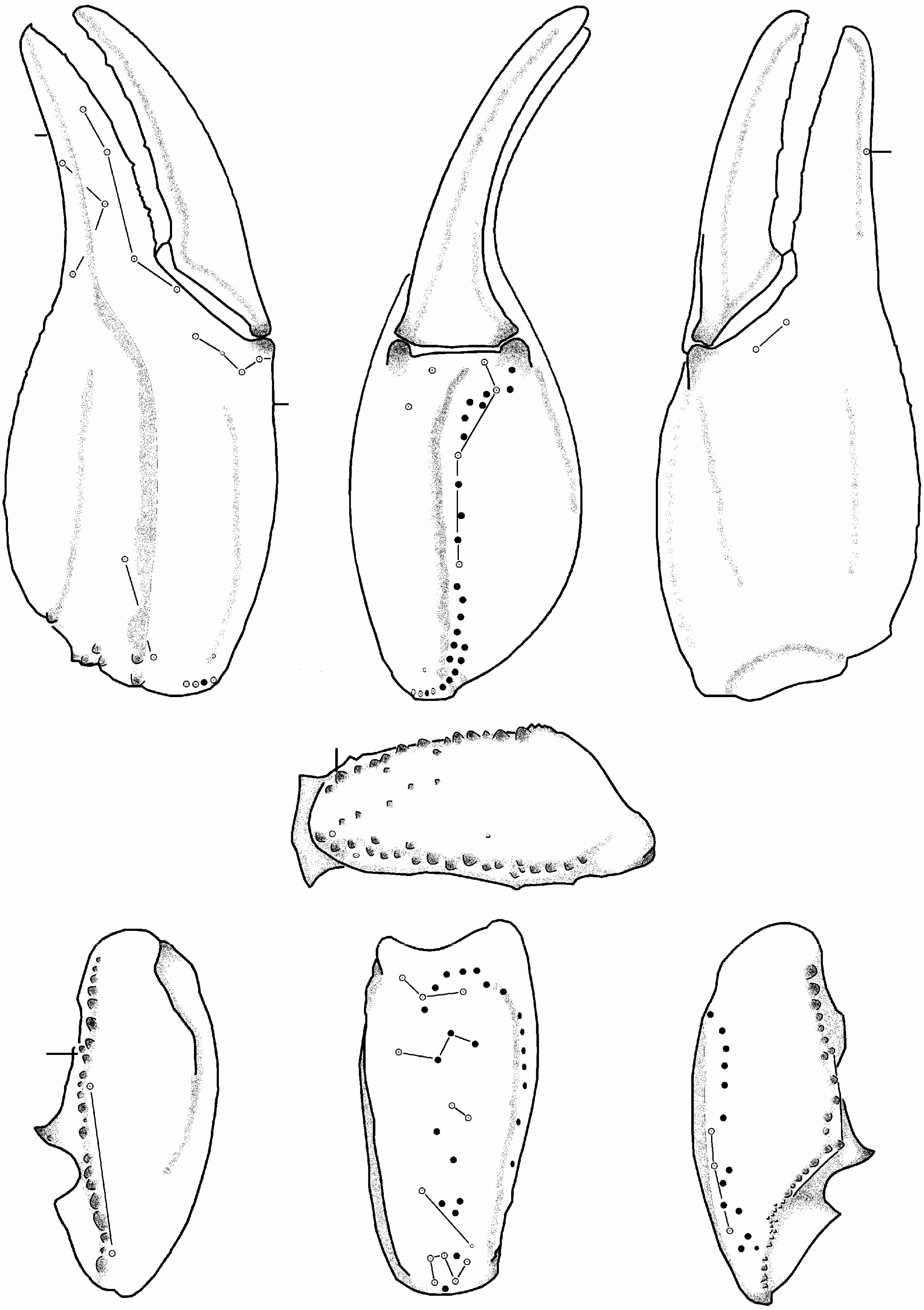


Fig. 29: Trichobothrial pattern of *Anuroctonus pococki pococki*, male holotype. Chela (top), external, ventral and internal views. Femur (middle), dorsal view. Patella (bottom), dorsal, external and ventral views. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

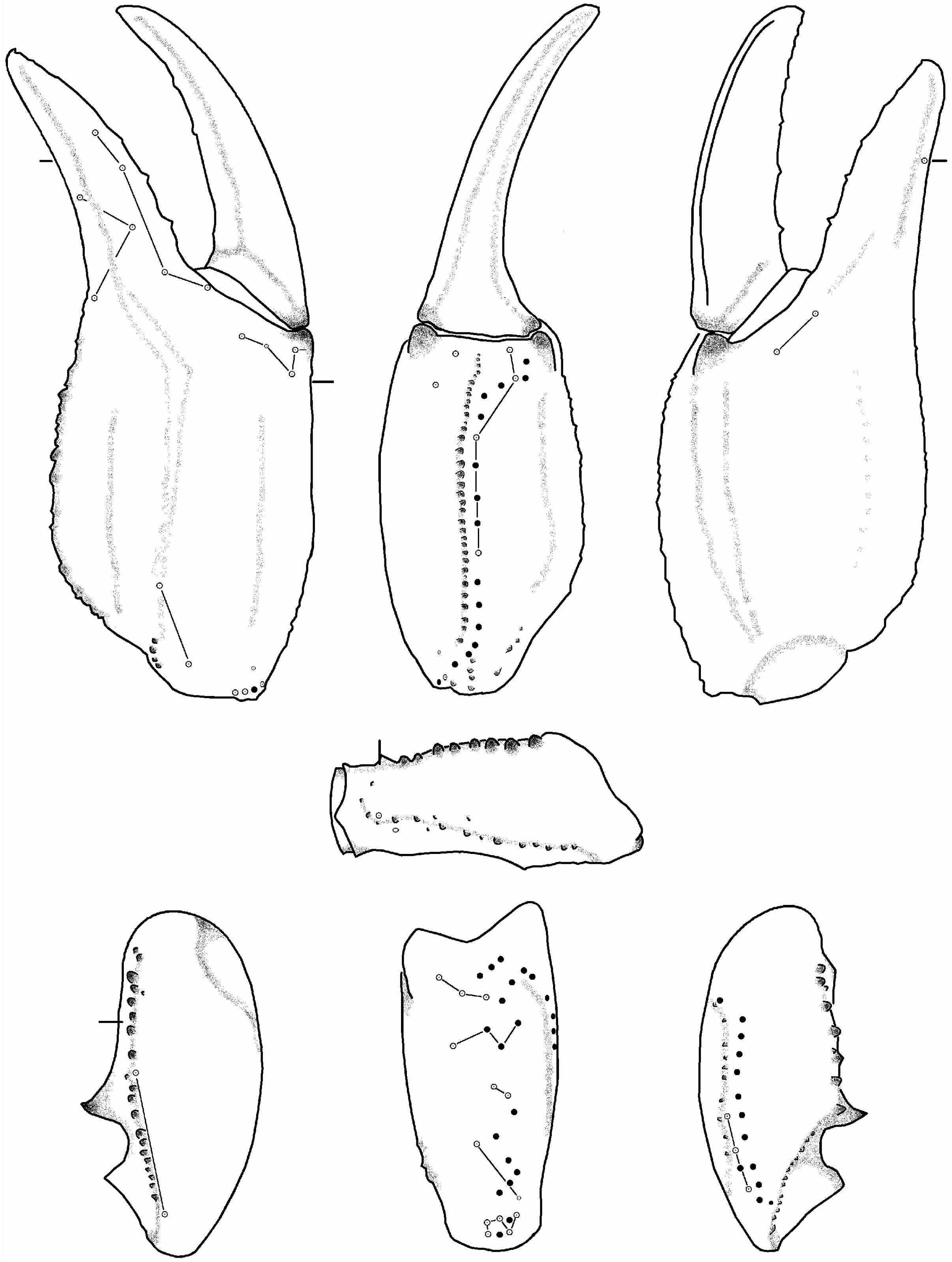


Fig. 30: Trichobothrial pattern of *Anuroctonus pococki bajae*, male holotype. Chela (top), external, ventral and internal views. Femur (middle), dorsal view. Patella (bottom), dorsal, external and ventral views. Open circles depict orthobothriotaxy; closed circles depict hypothesized accessory trichobothria.

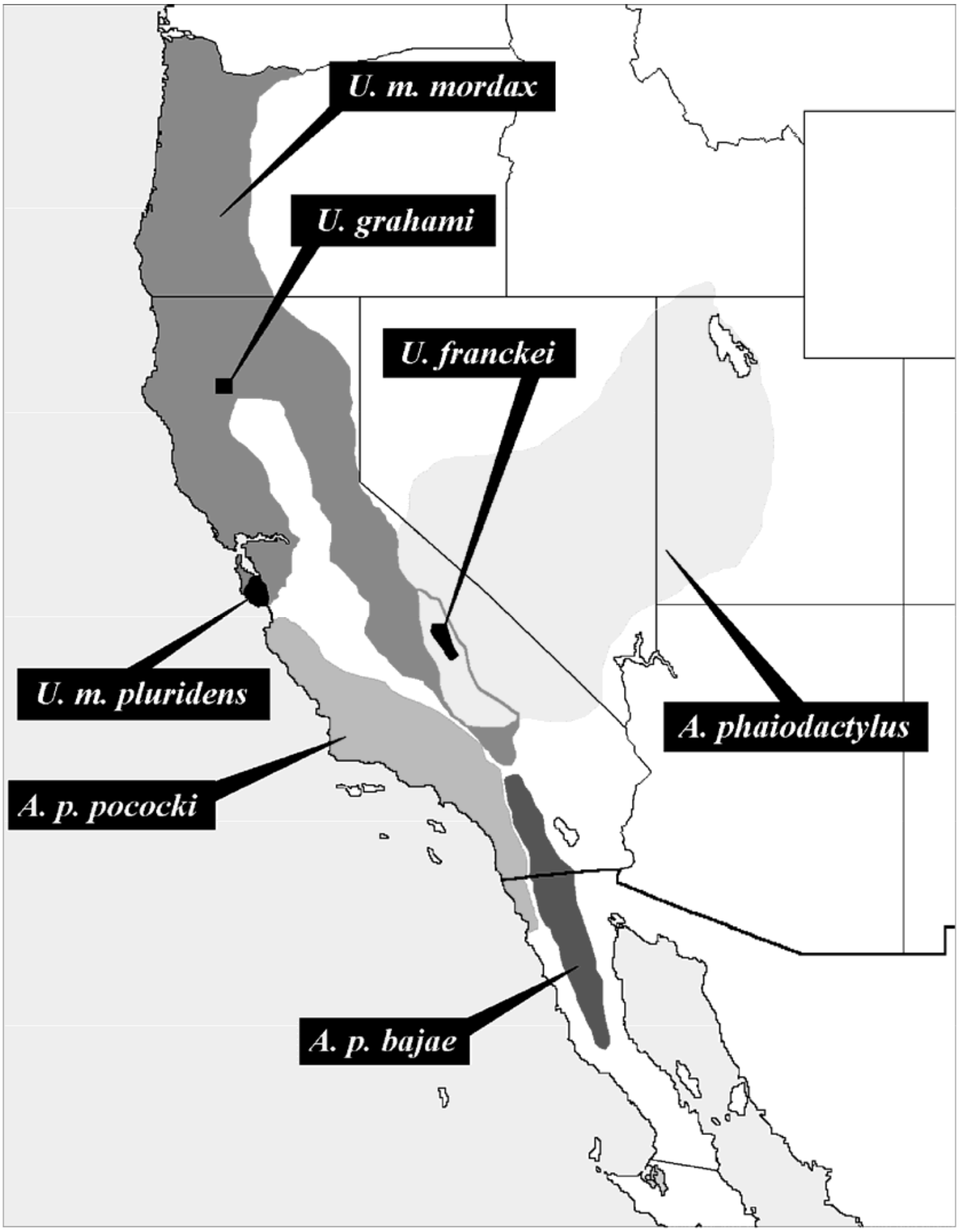
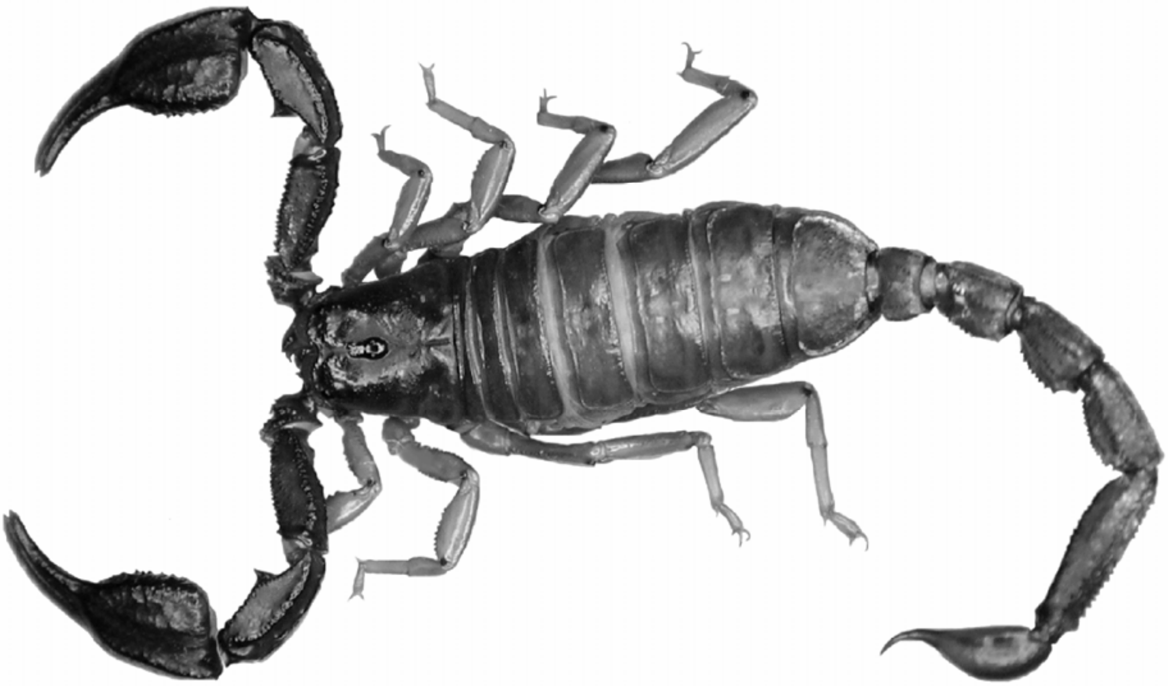


Fig. 31: Distribution of species and subspecies of chactid subfamily Uroctoninae in Southwestern United States and Baja California Norte, Mexico. Genera: *U* = *Uroctonus* and *A* = *Anuroctonus*. *Uroctonus* distribution based on Gertsch & Soleglad (1972), Hjelle (1972), and Williams (1986). *Anuroctonus* distribution based on specimens examined in this study.



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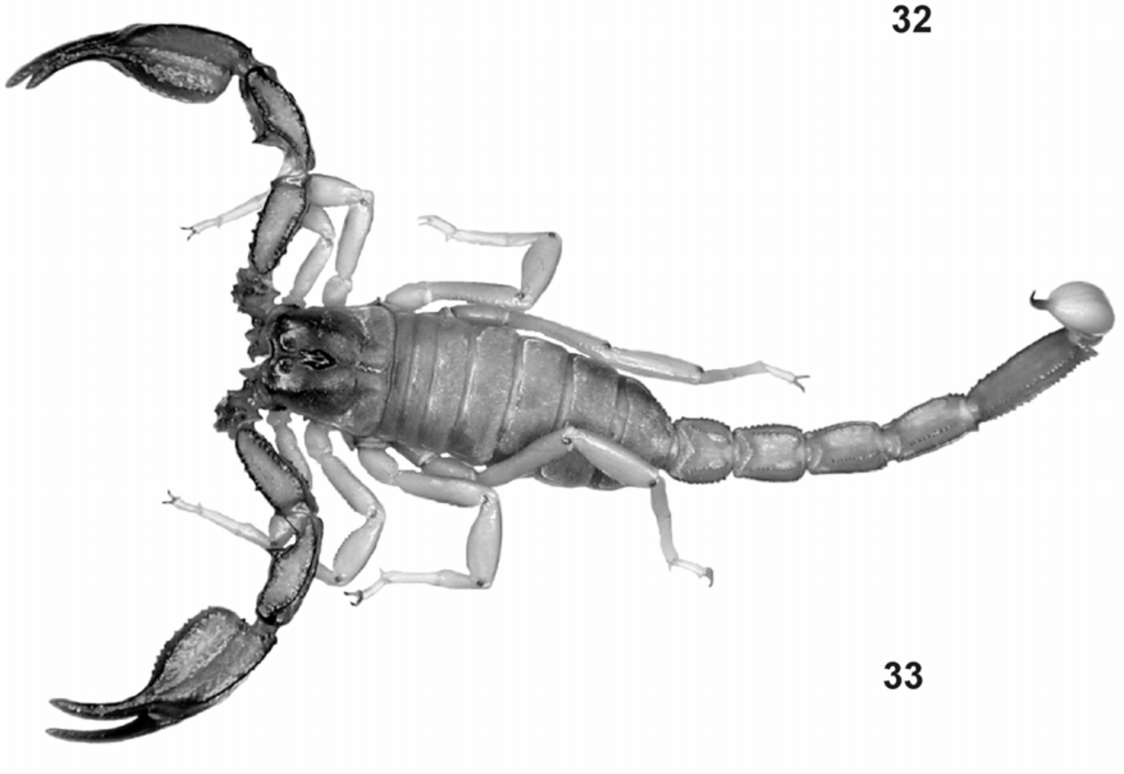

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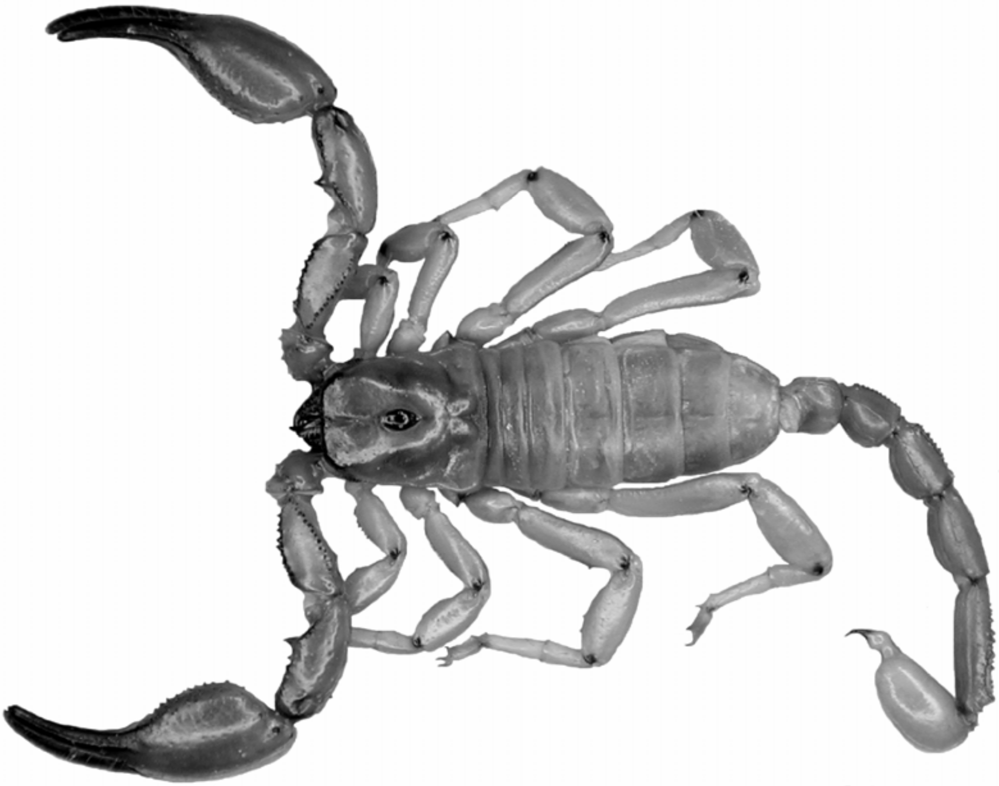
Fig. 32–33: Dorsal view. **32.** *Uroctonus mordax mordax* Thorell, female. Yosemite National Park, Mariposa Co., California, USA **33.** *Uroctonus mordax pluridens* Hjelle, male. Santa Clara, Santa Clara Co., California, USA.



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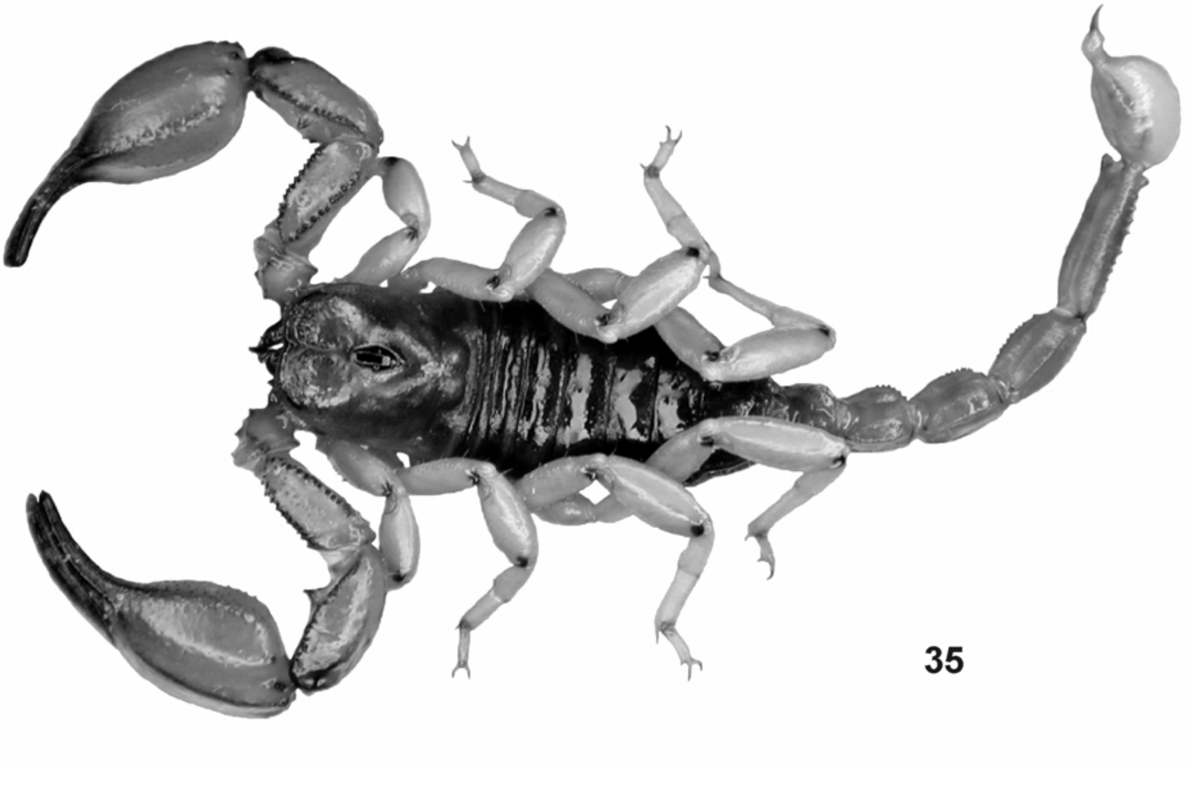

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Fig. 34–35: Dorsal view. **34.** *A. phaiodactylus* (Wood), male. Garrison, Beaver Co., Utah, USA. **35.** *A. pococki pococki*, male. Santee, San Diego Co., California, USA.

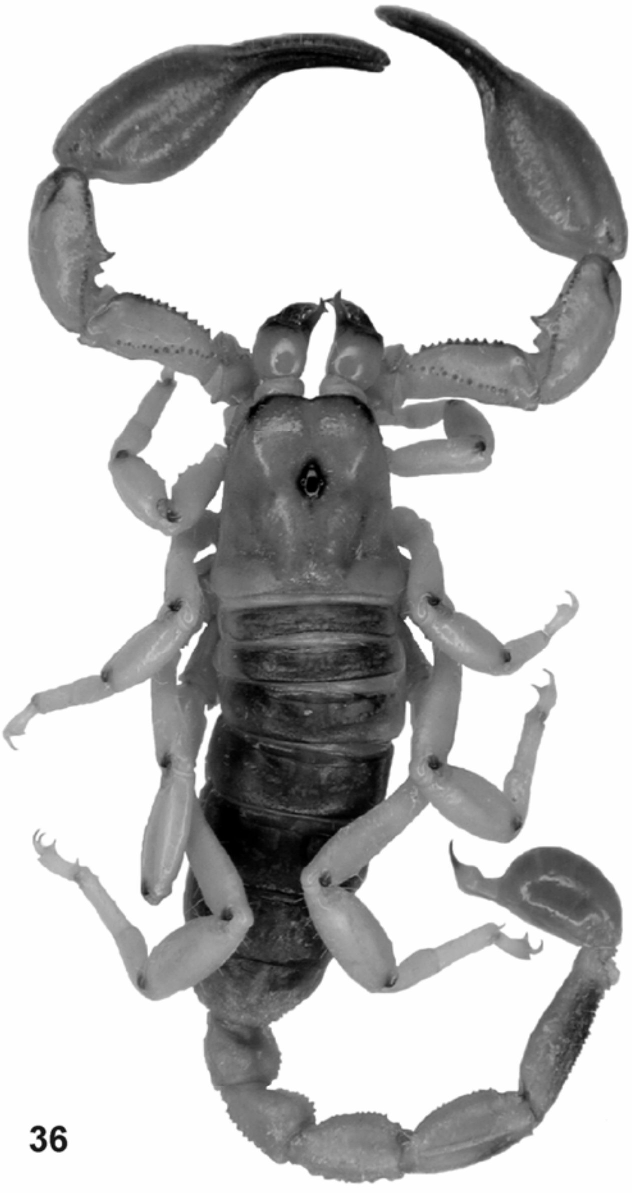

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Fig. 36: Dorsal view of *Anuroctonus pococki bajae*, male holotype. Ojos Negros, Baja California Norte, Mexico.

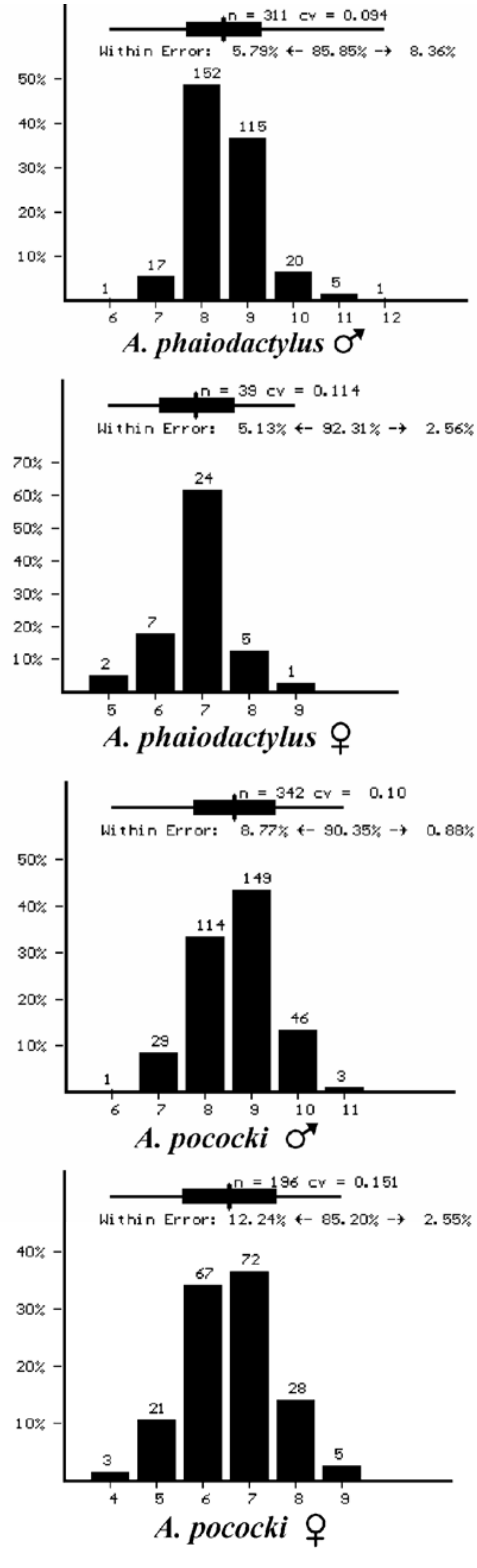

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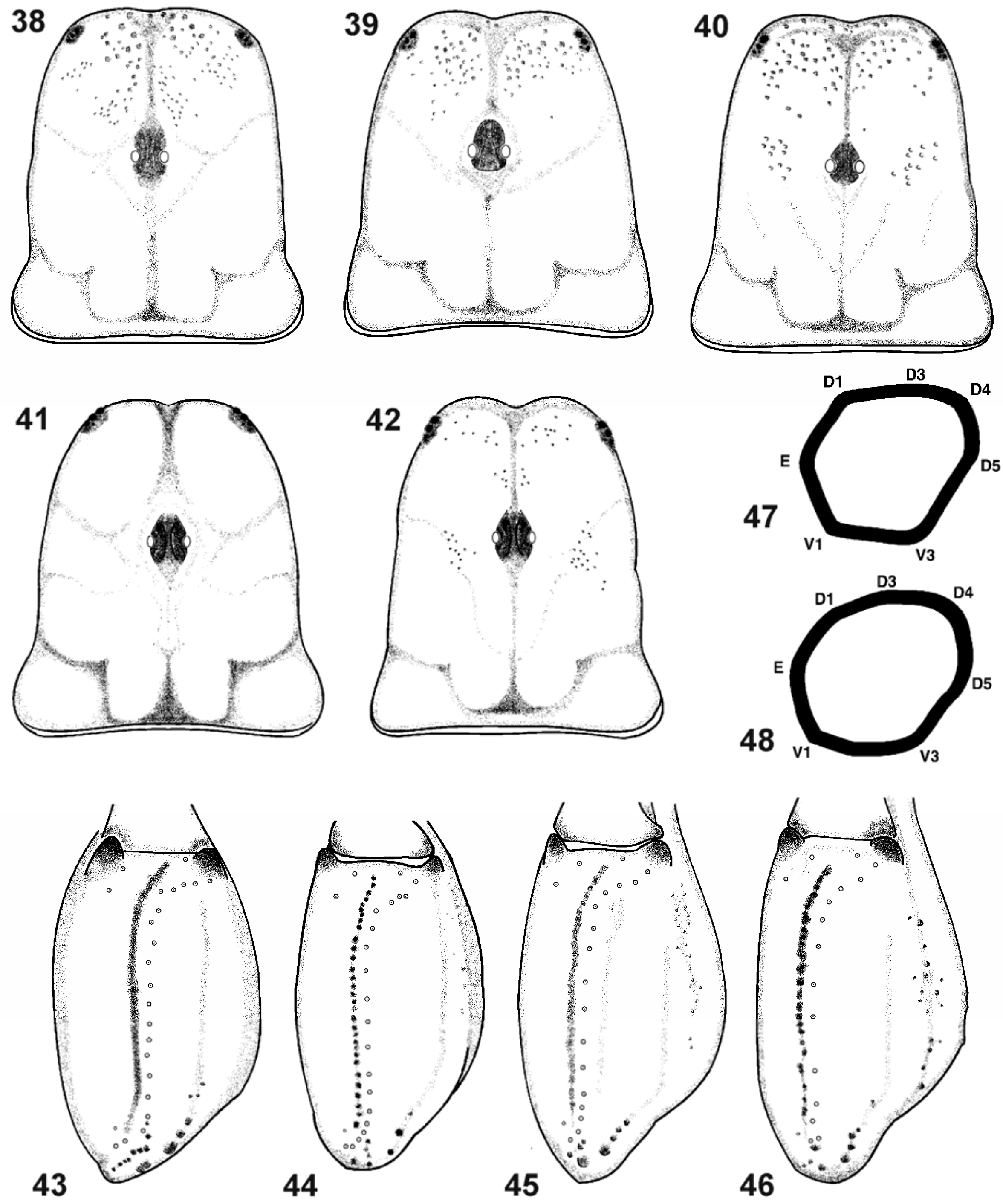
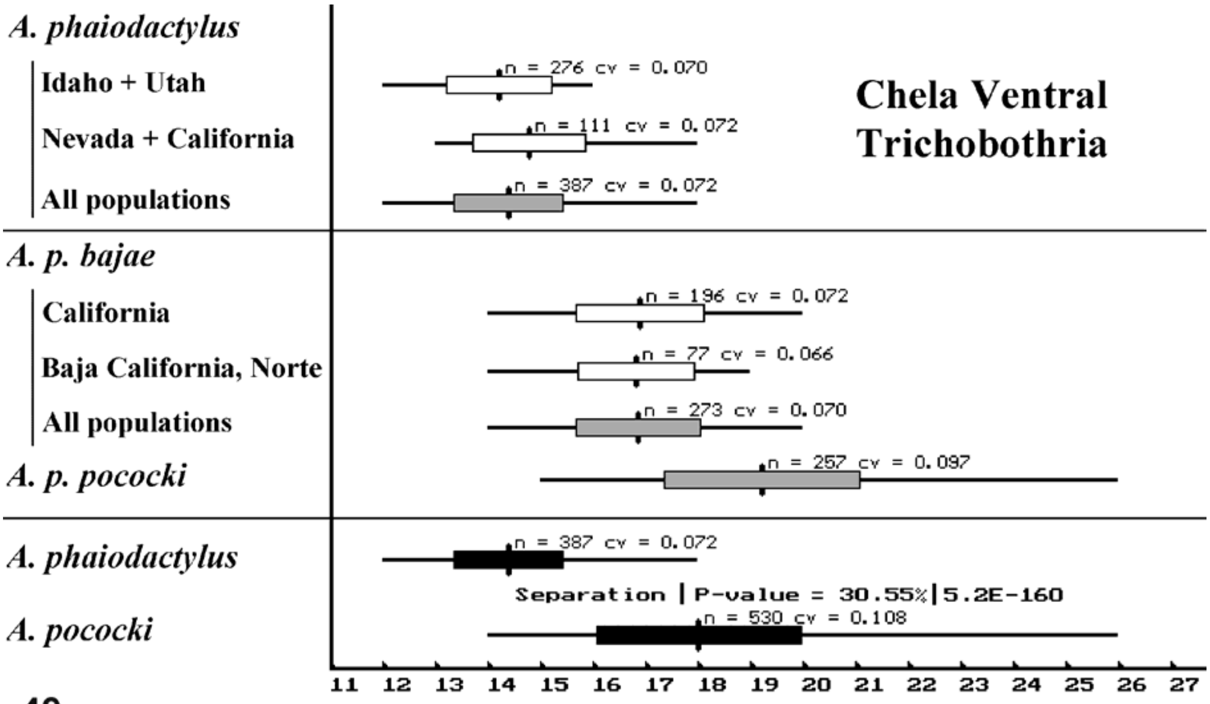
Fig. 37: Pectinal tooth count distribution for species of *Anuroctonus*. Horizontal bar: minimum, maximum, corrected minimum/maximum (mean-*SD* and mean+*SD*), and mean; *n* = number of samples, *cv* = coefficient of variability (*SD*/mean); vertical bars: percentage per count, number of samples per count on top and count value on bottom.



Figs. 38–48: 38–42. Dorsal view of carapace showing differences in granulation of interocular area in *Anuroctonus* species and subspecies (male). **43–46.** Ventral view of pedipalp chela showing ventroexternal carina (*V1*) development in *Anuroctonus* species and subspecies. **47–48.** Diagrammatic view of pedipalp chela showing the relative development of the digital (*D1*) carina (view from the fingers). **38.** *Anuroctonus pococki pococki*, Santee, San Diego Co., California, USA. **39.** *A. p. bajae*, Ojos Negros, Baja California Norte, Mexico. **40.** *A. p. bajae*, Pinyon Mountains, ABDSP, California, USA. **41.** *A. phaiodactylus*, Garrison, Beaver Co., Utah, USA. **42.** *A. phaiodactylus*, Saline Valley, Inyo Co., California, USA. **43.** *Anuroctonus pococki pococki*, male, Santee, San Diego Co., California, USA. **44.** *A. p. bajae*, male holotype, Ojos Negros, Baja California Norte, Mexico. **45.** *A. p. bajae*, male, Pinyon Mountains, ABDSP, California, USA. **46.** *A. phaiodactylus*, male, Garrison, Beaver Co., Utah, USA. **47.** *A. p. bajae*, male, Jasper Trail, ABDSP, California. **48.** *A. phaiodactylus*, male, Holbrook, Oneida Co., Idaho, USA.



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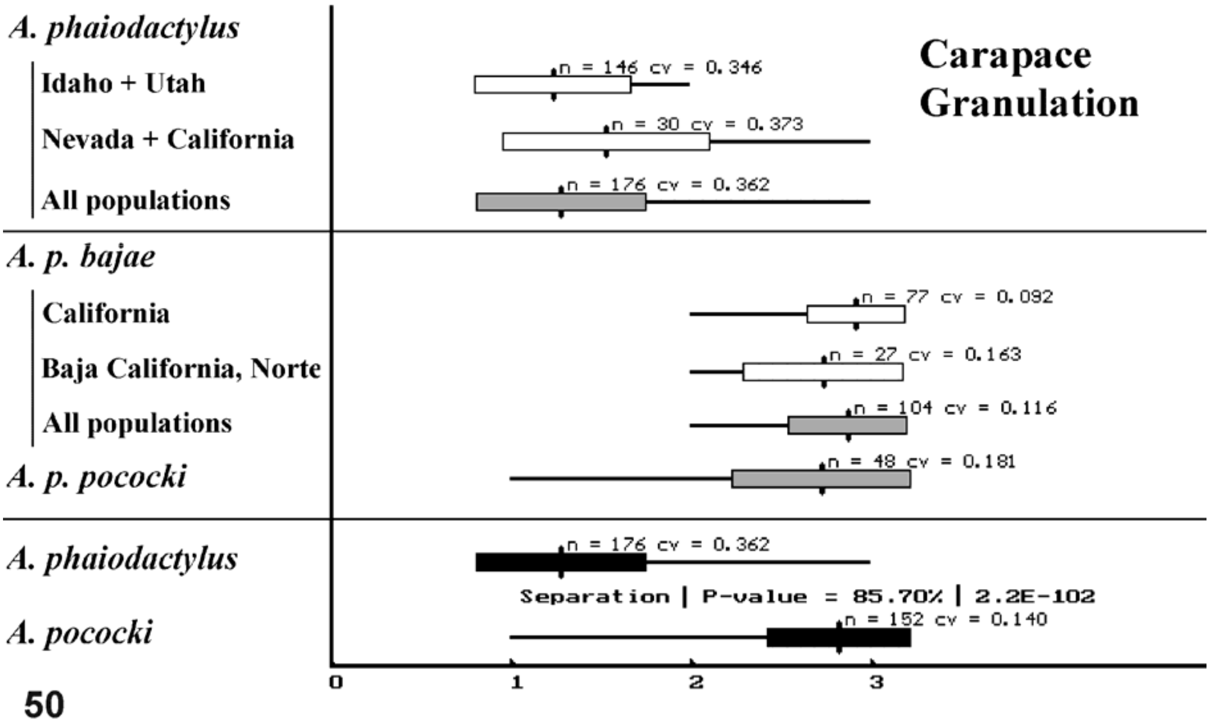

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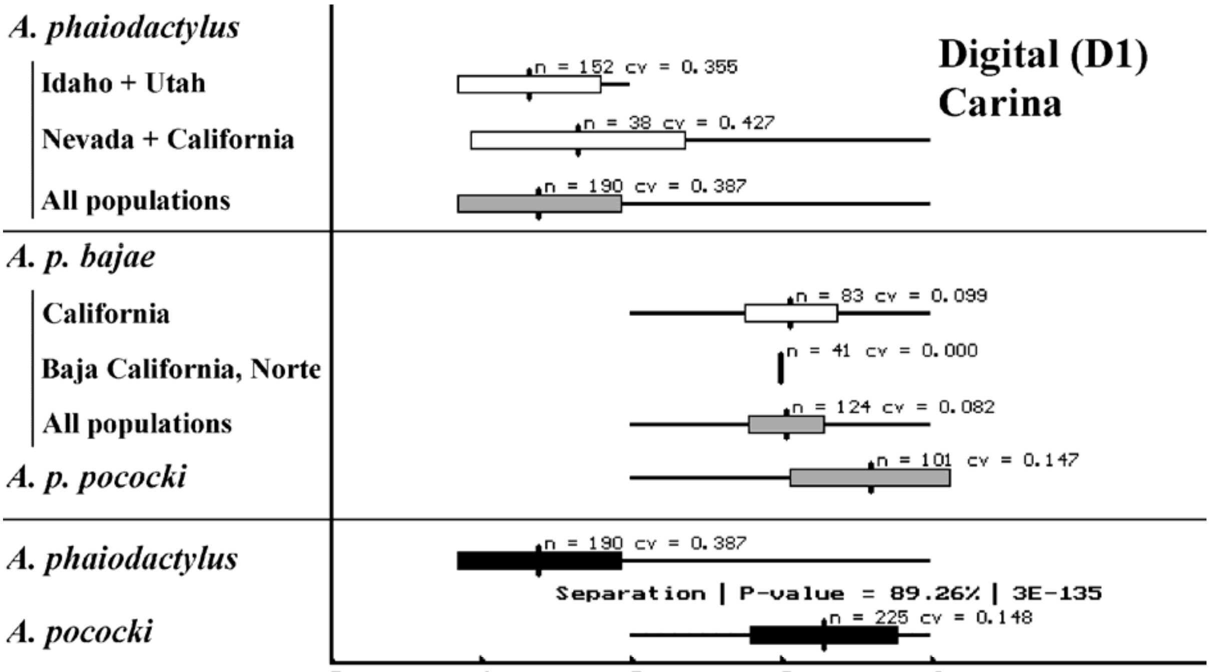
Fig. 49: Statistical distribution of pedipalpal *chela ventral trichobothria* counts for genus *Anuroctonus*. Degree of statistical difference between species *A. phaiodactylus* and *A. pococki* is indicated by plus-minus standard error range separation and the negligible variance analysis value (*p-value*). Horizontal bar: minimum, maximum, corrected minimum/ maximum (mean-*SD*/mean+*SD*), and mean; *n* = number of samples, *cv* = coefficient of variability (SD/mean).

Fig. 50: Statistical distribution of degrees of *carapace granulation of interocular area* for genus *Anuroctonus* (males only). Code values: ***1*** = smooth; ***2*** = smooth, anterior edge rough to granulate; ***3*** = light to heavy granulation. Degree of statistical difference between species *A. phaiodactylus* and *A. pococki* is indicated by plus-minus standard error range separation and the negligible variance analysis value (*p-value*). See Fig. 49 for definition of terms.



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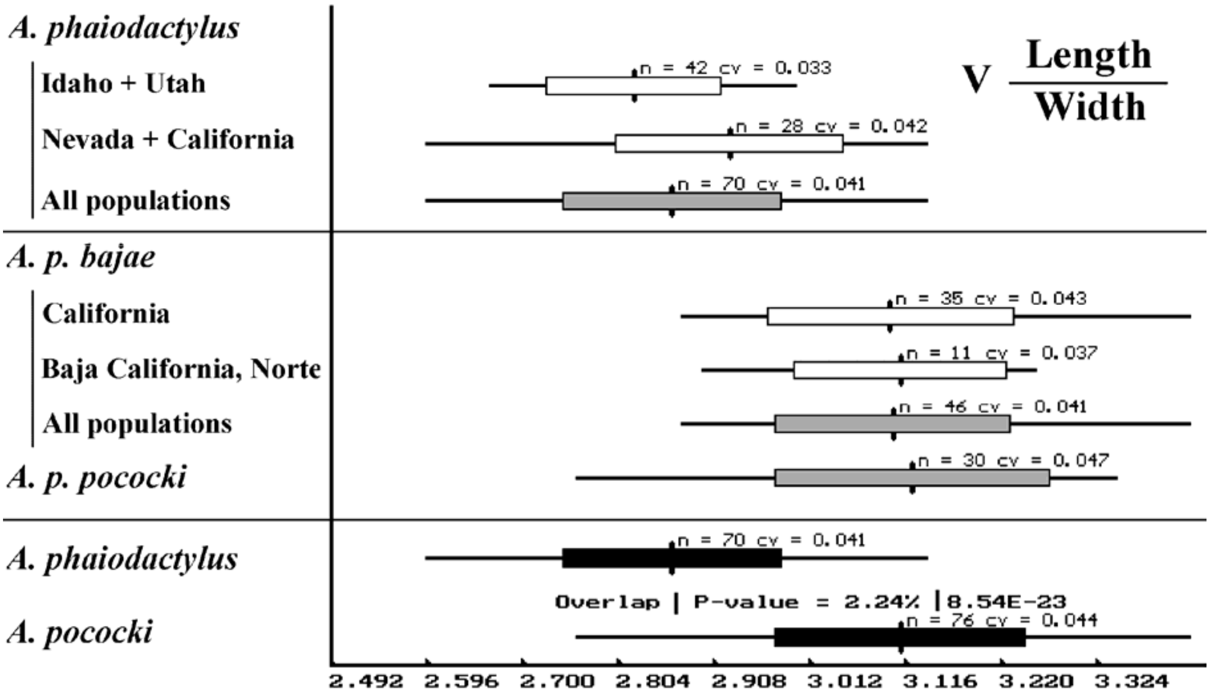

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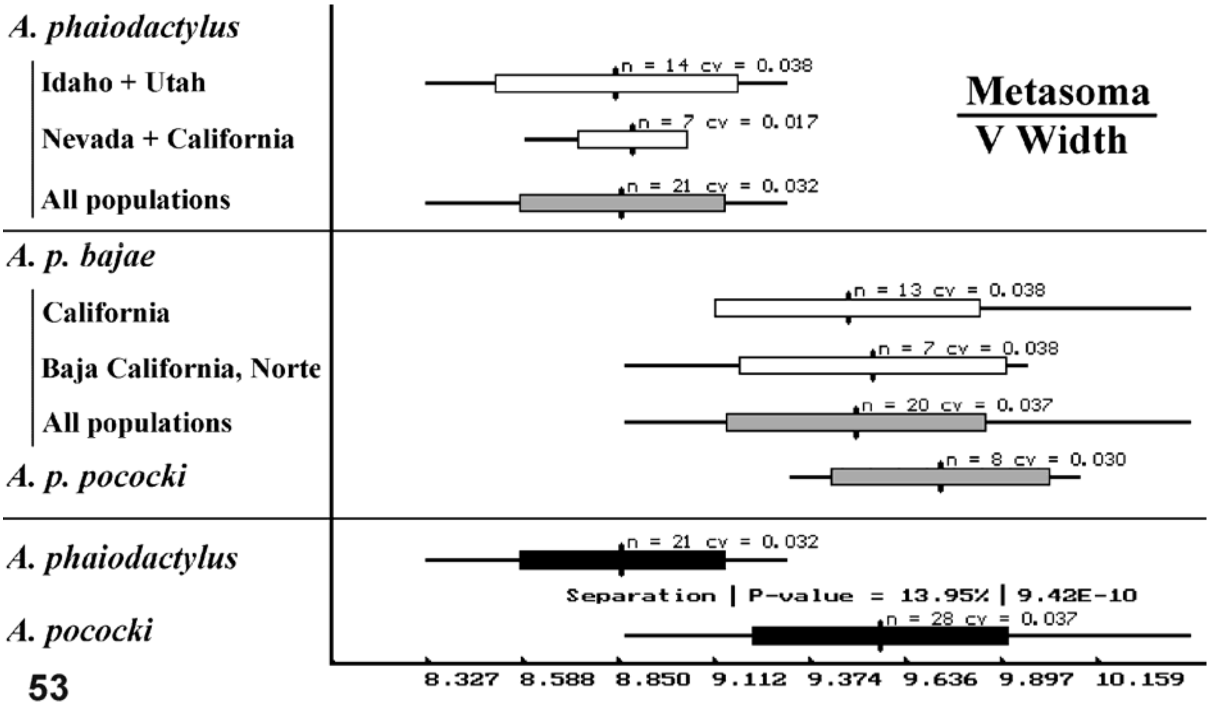
Fig. 51: Statistical distribution of degrees of *chelal digital (D1) carina development* for genus *Anuroctonus*. Code values: ***1*** = obsolete to weak; ***2*** = weak to rounded; ***3*** = strong, light to no pigmentation; ***4*** = strong, conspicuously pigmented. Degree of statistical difference between species *A. phaiodactylus* and *A. pococki* is indicated by sizable plus-minus standard error range separation and the negligible variance analysis value (*p-value*). See Fig. 49 for definition of terms.

Fig. 52: Statistical distribution of morphometric ratio *metasomal segment V length/width* for genus *Anuroctonus* (males only). Degree of statistical difference between species *A. phaiodactylus* and *A. pococki* is indicated by negligible plus-minus standard error range overlap and variance analysis value (*p-value*). See Fig. 49 for definition of terms.



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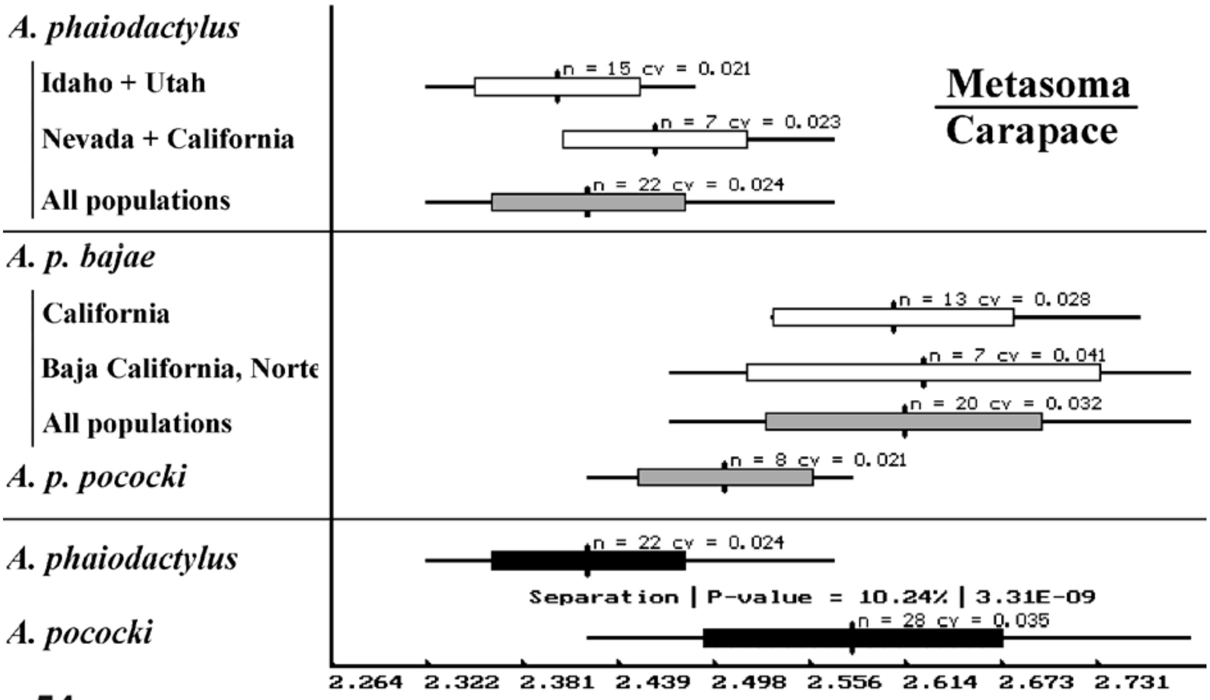

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Fig. 53: Statistical distribution of morphometric ratio *metasomal length/segment V width* for genus *Anuroctonus* (males only). Degree of statistical difference between species *A. phaiodactylus* and *A. pococki* is indicated by plus-minus standard error range separation and negligible variance analysis value (*p-value*). See Fig. 49 for definition of terms.

Fig. 54: Statistical distribution of morphometric ratio *metasomal length/carapace length* for genus *Anuroctonus* (males only). Degree of statistical difference between species *A. phaiodactylus* and *A. pococki* is indicated by plus-minus standard error range separation and negligible variance analysis value (*p-value*). See Fig. 49 for definition of terms.

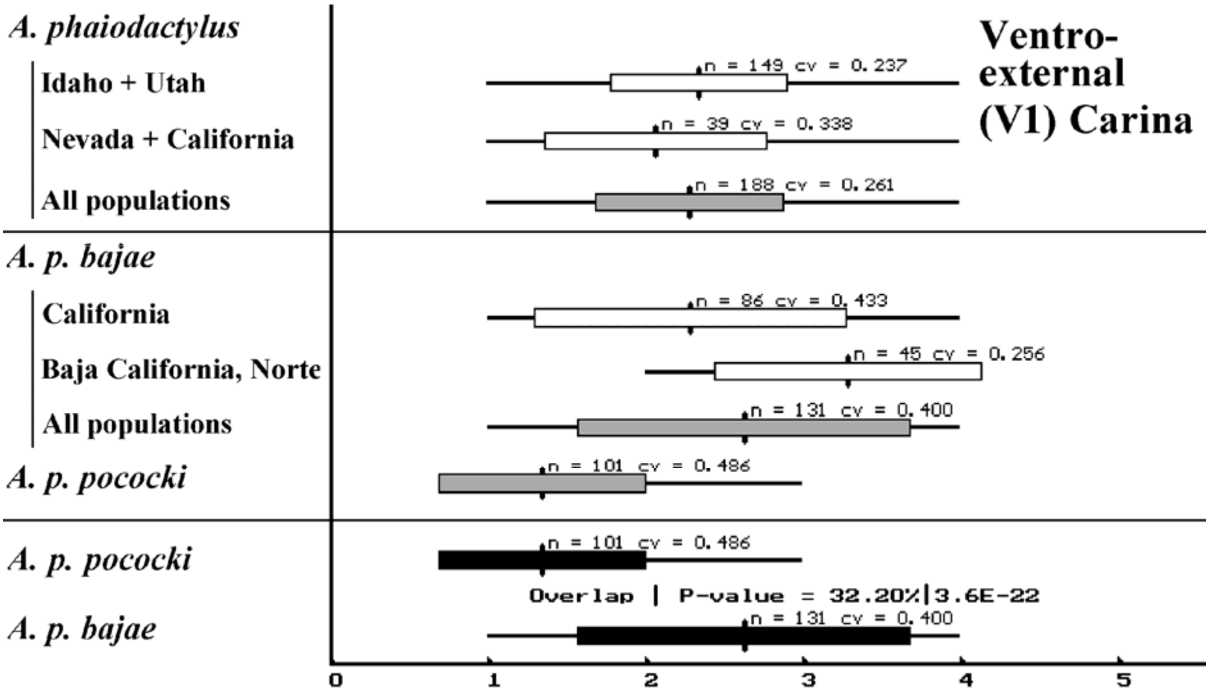

Fig. 55: Statistical distribution of degrees of *chelal ventroexternal (V1) carina development* for genus *Anuroctonus*. Code values: ***1*** = smooth and shiny; ***2*** = rough to pitted; ***3*** = pitted to granulate; ***4*** = distinctly granulate. Degree of statistical difference between subspecies *A. pococki pococki* and *A. p. bajae* is indicated by plus-minus standard error range overlap and the small variance analysis value (*p-value*). See Fig. 49 for definition of terms.

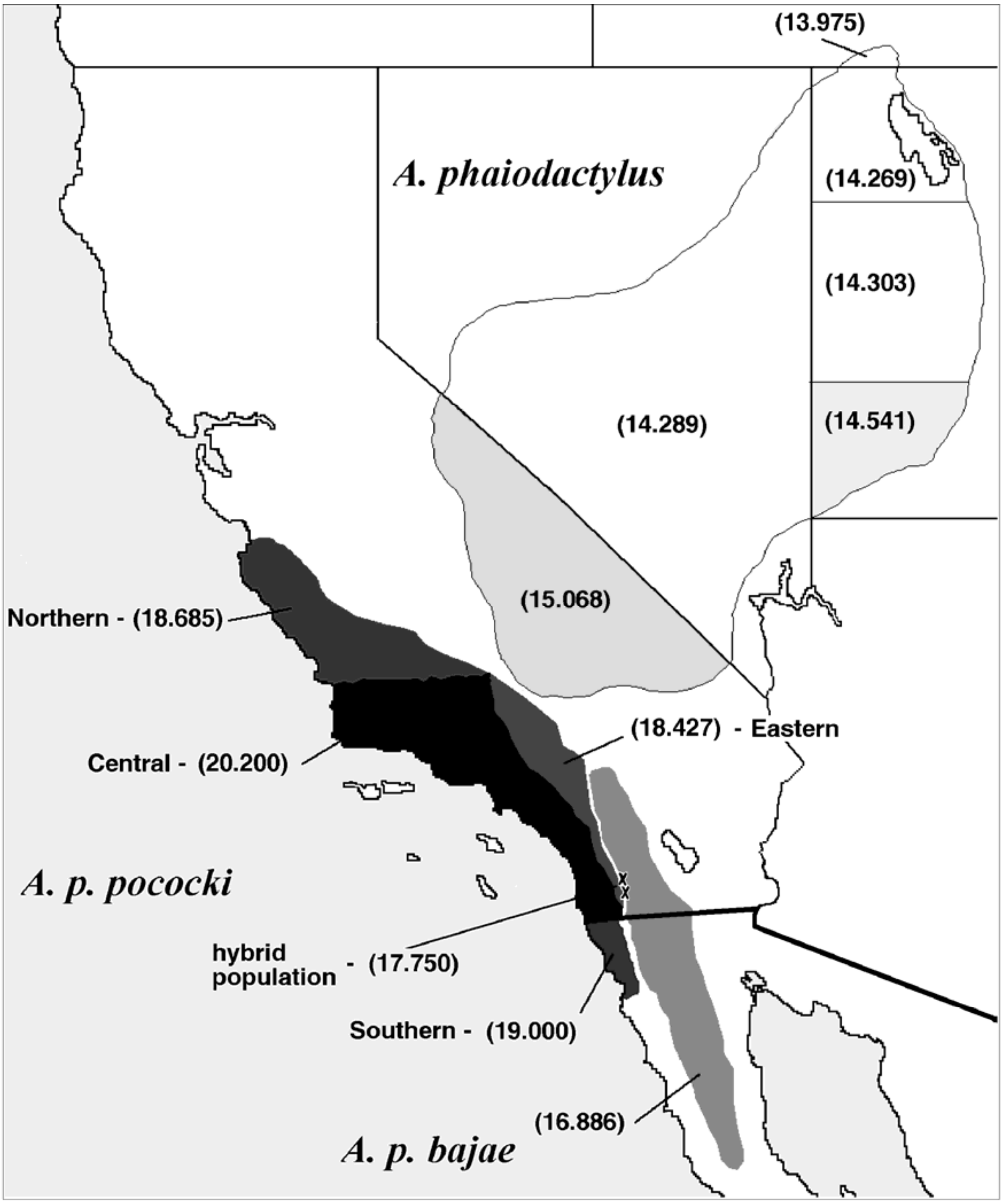

Fig. 56: Distribution of *Anuroctonus* species and subspecies in Southwestern United States and Baja California Norte, Mexico showing the *reduction* in counts of chelal ventral trichobothria as it presumably corresponds to speciation and species/subspecies radiation. For each area, the mean value is provided (in parentheses) and the shade of gray used is *proportional* to the mean value of that area (i.e., 256 shades of gray as it relates to a mean value range of 13.975 (assigned 255 = *white*)–20.200 (assigned 0 = *black*). *A. p. pococki* is divided into four populations in California: **Central** = coastal Los Angeles, Orange, Riverside (west), and San Diego (west) counties; **Northern** = Monterey, San Benito, San Luis Obispo, Santa Barbara, and Ventura counties; **Southern** = coastal Baja California Norte, Mexico; **Eastern** = Tulare (west), Kern (west), Riverside (east), and San Diego (east) counties. 'X' denotes subspecies hybridization. *A. phaiodactylus* is divided into six populations, California, Nevada, Idaho, and Utah which is divided further into three areas: **Southern** = Beaver, Washington, and Iron counties; **Central** = Utah and Millard counties; **Northern** = Box Elder and Tooele counties.