# New Genera and Species of Cribellate Coelotine Spiders from California (Araneae: Amaurobiidae) 

Darrell Ubick<br>Department of Entomology, California Academy of Sciences, 875 Howard Street<br>San Francisco CA 94103; Email: dubick@calacademy.org


#### Abstract

Two new amaurobiid genera, and three new species, are described from California. Parazanomys, with its single species, $P$. thyasionnes, is known from a few localities in Tulare County, and Cavernocymbium, which includes C. vetteri and C. prentoglei, from the Mojave Desert area. These small cribellate spiders exhibit very unusual genitalia, with complex retrolateral furrows on the male cymbium, a tripartite retrolateral tibial apophysis, and long coiled copulatory ducts in the vulva. On the basis of several synapomorphies with Draconarius Ovtchinnikov 1999 and related genera, these spiders are considered members of the Coelotinae. These genera also appear to be related to the amaurobiid genus Zanomys Chamberlin 1948, which is transferred to the Coelotinae. Being cribellates, the zanomyines appear to be basalmost coelotines, and thus force a reinterpretation of Wang's (2002) phylogenetic analysis.


Keywords: Amaurobiidae, Coelotinae, Parazanomys, Cavernocymbium, taxonomy, California

The Californian fauna is well known for its relictual biota. In terms of spiders, both the basal mygalomorphs (Antrodiaetidae and Mecicobothriidae) and araneomorphs (cribellates and haplogynes) are richly represented in this region. For example, the number of cribellate taxa present in California, some 20 genera and 120 species, exceeds all comparably sized regions with the notable exception of New Zealand. This paper presents additional cribellate taxa to the inventory, the two genera and three species described below.

This project began over 10 years ago when I first collected specimens of a small cribellate spider and was immediately struck by a most unusual modification of the cymbium, which bears, along its dorsal surface, a retrolateral groove enclosing a flattened glabrous region (Figs. 15c-d). A search through the literature of Nearctic spiders failed to turn up species with a similar morphology and, believing the species to be an introduction from some exotic locality, the project was shelved. It was resurrected a few years ago after receiving specimens from Rick Vetter, Wendell Icenogle, and Tom Prentice of additional small cribellates representing two species with different but likewise bizarre cymbia. Although resembling the first species in having retrolateral modifications on the cymbium, these two have instead a deep lateral cymbial pocket [Figs. 16c-d, 17c-d]). Now with three known species, all collected from undisturbed habitats, there seems little doubt that these unusual spiders are native elements of the California fauna.

## Methods

Specimens were studied using a Leica MZ12.5 dissecting scope, Nikon SL3D compound scope, and Leica M420 dissecting scope equipped with a JVC KY-F70B digital camera and a

Syncroscopy Auto Montage system. Specimens were prepared for scanning by cleaning in a Branson 1510 Ultrasonicator, dried with a Denton DCP1 Critical Point Dryer, coated with AuPd with a Denton Vacuum Desk II Sputter Coater, and examined with a Hitachi S-520 Scanning Electron Microscope.

Abbreviations: ALE $=$ anterior lateral eye(s), ALS $=$ anterior lateral spinnerets, $\mathrm{AME}=$ anterior median eye(s), DTA = dorsal tibial apophysis, MA = median apophysis, OAL = ocular area length, $\mathrm{PER}=$ posterior eye row, $\mathrm{PLE}=$ posterior lateral eye(s), PLS = posterior lateral spinnerets, PME $=$ posterior median eye(s), PMS $=$ posterior median spinnerets, RTA $=$ retrolateral tibial apophysis.

Depositories: CAS $=$ California Academy of Sciences, San Francisco; CDFA $=$ California Department of Food and Agriculture, Visalia; CDU $=$ collection of D. Ubick, CTP $=$ collection of T. Prentice, CWI = collection of W. Icenogle; UCR = University of California, Riverside.

Appendage measurements are given as: total length (femur, patella + tibia, metatarsus, tarsus). All lengths are in mm.

## TAXONOMY

## Zanomyine Complex

DIAGNOSIS.- This group shares the following characters: sexually dimorphic carapace (circular in males, piriform in females), male cymbium with retrolateral groove or pocket, male cymbium lacking trichobothria, male palpal retrolateral apophysis with 2 or 3 prongs, AME small or absent, cribellum divided.

Included genera.- Zanomys Chamberlin, 1948; Parazanomys, gen. nov.; Cavernocymbium, gen. nov.

## Genus Parazanomys, Ubick, gen. nov.

Type species: Parazanomys thyasionnes, Ubick, sp. nov.
Diagnosis.- This genus can be separated from most Nearctic cribellate amaurobiids, except Zanomys, by its small size and darkly pigmented body. The male differs from that of Zanomys (Fig. 18) in having a tripartite RTA, a long cymbial furrow, a long threadlike embolus, and the presence of an additional tegular process (Fig. 15). The female differs from Zanomys in having transversely coiled copulatory ducts (Figs. 10c-d).

Etymology.- The generic name refers to the presumed relationship with the genus Zanomys and is neuter in gender.

Description.- Small cribellate spiders, $1.94-3.30$ in total length. Body pigmented with chevron pattern on abdomen (Fig. 1). Carapace piriform in females, sub-circular in males; glabrous with some erect setae on cephalic region. Fovea narrow, longitudinal. Eyes eight in two procurved rows; AME smallest, from $1 / 3$ to $1 / 2$ diameter of PME. Clypeus about $1 / 2$ diameter of ALE.

Chelicera with small boss, slightly geniculate in female, retromargin with 5 teeth, promargin with 3-4. Sternum anteriorly truncate, posteriorly extended between coxae IV, posterior extension about half coxal width; endites angular, slightly convergent, labium wider than long, one half length of endites.

Abdomen with epigastric furrow of male lacking epiandrous spigots. Female with epigynum a convex plate with lateral copulatory openings; copulatory ducts arranged in transverse switchback coiling (Fig. 10). Tracheal system with median and lateral trunks, both moderately branched, restricted to abdomen (Fig. 4). Spinnerets with divided cribellum, non-functional in male; ALS largest, twice diameter of PLS; ALS with 3 piriform spigots, 1 major ampullate (in female); PMS
with 1 aciniform spigot, 1 cylindrical spigot (in female), 1 paracribellar spigot (in female); PLS with 3 aciniform spigots, 1 cylindrical spigot (in female), 3 paracribellar spigots (in female) (Fig. 5).

Legs with weak spines, absent on anterior legs: tibiae: III, IV v0-0-2; metatarsi: III, IV p0-0$1, \mathrm{~d} 0-0-1$ or d0-1-1. Calamistrum occupying about one-half length of metatarsus IV. Tarsi with 2 , metatarsi with 3 dorsal trichobothria, distal trichobothria long, bent; trichobothrial base with fine striations resembling the abdominal cuticle (Fig. 8c); tarsi with three claws. Leg formula 1423 (male) or 4123 (female).

Male palpus lacking tarsal trichobothria; cymbium large, bearing retrolateral groove encircling flattened glabrous region; tibia with ventral, dorsal and 3-pronged retrolateral apophyses; bulb with long, threadlike embolus, complex conductor, median apophysis, and distal tegular process.

Included species.- Only Parazanomys thyasionnes.
Distribution.- Tulare Co., California.

## Parazanomys thyasionnes, Ubick, sp. nov.

Figs. 1, 4-5, 8c, 9-10, 15; Map 1.
Type material.- Holotype male and allotype female from Twin Buttes, Tulare County, California, collected under granite boulder in grassland on the NE slope of the western butte, on 29 March 1991 by D. Ubick; deposited in CAS.

Etymology.- The specific name honors Bill Tyson and Dennis Haines for their efforts in collecting these elusive spiders.

Diagnosis.- Same as for genus.
Description.- Male (holotype, range of other males in parentheses; $\mathrm{N}=5$ ): Total length 2.22 (2.02-2.30). Carapace length 1.08 ( $0.95-1.10$ ), width 0.90 ( $0.86-0.93$ ); clypeus 0.09 . Sternum length 0.60 , width 0.50 ; labium length 0.13 , endite length 0.35 . Abdomen length 1.12 , width 0.82 . Eye diameters and interdistances: AME 0.02, ALE 0.06, PME 0.06, PLE 0.06; AME-AME 0.02, AME-ALE 0.02, PME-PME 0.05, PME-PLE 0.04, ALE-PLE 0.03, AME—ALE 0.02; PER 0.29 , OAL 0.17. Appendages: palp- $1.46(0.44,0.30,0,0.72)$; leg I—3.52 (1.10, 1.22, $0.78,0.42$ ); leg II-2.76 ( $0.84,0.98,0.52,0.42$ ); leg III-2.32 ( $0.70,0.78,0.50,0.34$ ); leg IV—3.22 (0.94, $1.14,0.72,0.42$ ); leg formula 1423.

Color: carapace yellowish brown, black around, between eyes, black maculations along thoracic groove, gray maculations along sides, fovea reddish; abdomen black with central pattern of 5 transverse pale chevrons, with numerous scattered small white spots, especially along sides. Legs brown with black annulations.

Carapace convex, circular in dorsal view; fovea long, about subequal to width of eye group; AME small, diameter $1 / 3$ that of other, subequal eyes; both rows procurved. Chelicerae with boss, retromargin with 5 subequal teeth, promargin with 3-4 teeth, subbasal largest, apical smallest.

Spinnerets with non-functional cribellum; ALS largest, separated by about one radius; PMS tiny; PLS about as long as ALS. ALS with 3 large piriform spigots and 1 nubbin; PMS with 1 aciniform spigot and 2 nubbins; PLS with 3 aciniform spigots and 5 nubbins. Calamistrum weakly represented in basal half of metatarsus IV.

Palpus (Fig. 15) large, complex; cymbium apically truncate, with retrolateral surface flattened, glabrous, with dorsal groove, lacking trichobothrium; bulb with articulating sickle-shaped median apophysis, apical membraneous conductor, and apical pointed tegular process; embolus threadlike, arising at base of bulb, curving around bulb. Tibia (Fig. 9) with 2 small ventral and 1 dorsal apophyses and a 3-pronged retrolateral apophysis, of which median prong appears to be flexibly attached.

Female (allotype, range of other females in parentheses; $\mathrm{N}=5$ ): Total length 2.84 (1.94-3.30). Carapace length $0.96(0.80-1.10)$, width $0.64(0.58-0.80)$; clypeus length 0.04 . Sternum length 0.58 , width 0.48 ; labium length 0.11 , endite length 0.27 . Abdomen length 1.96 , width 1.40 . Eye sizes and interdistances: AME 0.04, ALE 0.07, PME 0.06, PLE 0.07; AME—AME 0.01, AMEALE 0.015, PME-PME 0.05, PME-PLE 0.03, ALE-PLE 0.01; PER 0.30, OAL 0.16. Appendages: palp-1.14 ( $0.36,0.40,0,0.38$ ); leg I—2.80 ( $0.80,1.00,0.60,0.40$ ); leg II—2.36 ( $0.70,0.80,0.48,0.38$ ); leg III—2.10 ( $0.66,0.68,0.44,0.32$ ); leg IV—2.82 ( $0.82,1.00,0.64,0.36$ ); leg formula 4123.

Color: as in male except with additional markings on carapace (with gray band along thoracic groove and maculations along sides), abdomen with more pronounced chevron pattern and fewer white dots (Fig. 1a). Abdominal color ranges from yellowish to brown to greenish with black markings on all sides and, in some specimens, almost entirely black (Fig. 1b).

Carapace convex, piriform in dorsal view; fovea shorter than in male, about one-half width of eye group; AME small, diameter $1 / 2$ that of other, subequal eyes; both rows procurved. Chelicerae slightly geniculate, with boss; retromargin with 5 subequal teeth; promargin with 3-4 teeth, subbasal largest, apical smallest.

Spinnerets with divided cribellum; ALS largest, separated by about one radius, longer than PLS, almost twice their diameter; PMS tiny. ALS with 3 large piriform spigots, 1 smaller major ampullate spigot, and 2 nubbins; PMS with 1 aciniform, 1 cylindrical, and 1 paracribellar spigots; PLS with 3 aciniform, 1 cylindrical, and 3 paracribellar spigots (Fig. 5). Calamistrum a single row of curved setae occupying basal $3 / 5$ of metatarsus IV.

Epigynum convex, with pair of lateral copulatory openings and anterior pit; vulva with ducts in transverse switchback coiling and oval posteriolateral spermathecae (Fig. 10). Copulatory ducts ending in mesal blind sac, suggesting that embolus must reverse direction at that point (indicated as curved arrow in Fig. 10d) in order to reach lateral spermathecae.

Biology.- These spiders have been collected in a variety of biomes and elevations, from open grassland hills (at about 100 m elevation) to sequoia forests (at 2000 m ). Most of the collections are from intermediate localities, largely oak to oak-chaparral to mixed broadleaf evergreen forests. These cryptozoic spiders have been found under rocks and decomposing logs, in leaf litter, in moss from a roadcut, and from a flume. The specimens from the flume are all males, collected from March to June, which must have fallen into the channel somewhere along its 5 -mile course. As described by Halstead and Haines (1987), the flume flows through chamise chaparral and foothill woodland biomes at an elevation of 660 m . In the rocky grassland habitats, the spiders were found beneath granite boulders in February and March and would not be expected to occur much after that due the xeric conditions of the habitat. More recent collections were at higher elevations in oak, mixed broadleaf, and sequoia forests in April and November.

My field observations at Twin Buttes suggest that mating takes place during late autumn to winter as females with eggsacs were found in abundance from February to late March. At that time, the species was the most common spider on rock undersurfaces. Females were observed guarding eggsacs beneath loose, tent-like enclosures of silk. They were commonly positioned at the rock perimeter near the soil contact, often with several individuals at a single boulder. Most of the females collected were with eggsacs, some obviously gravid and positioned beneath silken tangles in a rock concavity and others, having apparently just deposited eggs, were carding cribellate silk on the sacs. Carding was in the typical entelegyne manner, by slow movement of braced fourth legs.

In the lab, the spiders were maintained in small ( 1 dram) vials where they soon constructed sheet webs from which they remained suspended. The webs are constructed of a fine mesh, which
seems to include some cribellate strands. The spiders readily captured and fed upon Psocoptera, Collembola, and Drosophila placed on the floor of the vial. Prey was captured using the bite and drag method and was usually pulled up into the sheet for feeding. Observations on a living male indicate that the embolus is held along the mesal surface of the bulb, and not in the cymbial furrow, so that the tip probably rests in the conductor. The male was placed with a female where he cohabited and fed for about a week and then died. No mating behavior was seen during this period. Females remained alive in captivity for several weeks.

Several females constructed eggsacs in captivity, suspending them by silk strands. These were white, lenticular structures with sharp edges and a central swelling containing the eggs. Given the opportunity, the spiders would cover the eggsac with small particles of dirt. In late May 2003 three eggsacs hatched and produced from 7-9 spiderlings each. These were maintained for a few months on a diet of small Collembola.

Other material examined.- Paratypes: CALIFORNIA: Tulare Co.: Ash Mountain, Kaweah Power Station \#3, $36^{\circ} 29^{\prime} 3.3^{\prime \prime} \mathrm{N}, 18^{\circ} 49^{\prime} 39.9^{\prime \prime} \mathrm{W}, 660 \mathrm{~m}$ el., ex flume, 13 April 1985 (R.D. Haines, CDFA), 1 male; 9 June 1986 (R.D. Haines, CDFA), 1 male; 28 March 1987 (P. Sherrill, CDFA), 2 males; 6 March 1993 (R.D. Haines, CDFA), 1 male; sifted from moss along roadcut in broadleaf evergreen forest, 27 April 2004 (D. Ubick, P. Paquin, CDU), 2 females, 2 juveniles; Bacon Hill, nr. Ivanhoe, $36^{\circ} 27^{\prime} \mathrm{N}, 19^{\circ} 10.7^{\prime} \mathrm{W}, 400-500$ ft. [120-150 m] el., 14 March 1990 (W. H. Tyson, CDFA), 1 male; Sequoia National Park, 2.7 km E Giant Forest Museum, $36^{\circ} 34^{\prime} 30.9^{\prime \prime} \mathrm{N}, 118^{\circ} 45^{\prime} 28.9^{\prime \prime} \mathrm{W}$, 2000 m el., under decomposing wood and sifting litter in Sequoia forest, 1 May 2004 (D. Ubick, P. Paquin, CDU), 1 male, 1 female; Sequoia National Park, S Fork Ranger Station, $36^{\circ} 20.9^{\prime} \mathrm{N}, 118^{\circ} 45.8^{\prime} \mathrm{W}, 3700 \mathrm{ft}$. [1200 m] el., oak forest, under rocks/in litter, 4 Nov 2004 (D. Ubick, CDU), 3 males, 3 females; Sequoia National Park, 2.8 km E Visitor Center, $36^{\circ} 30.4^{\prime} \mathrm{N}, 118^{\circ} 48.6^{\prime} \mathrm{W}$, 650 m , broadleaf forest; ex litter/rocks, 4 Nov 2004 (N. Dupérré, P. Paquin, D.Ubick, CDU, CAS), 2 males, 11 females; Twin Buttes, $36^{\circ} 26^{\prime} \mathrm{N}, 119^{\circ} 12^{\prime} \mathrm{W}$, 400-500 ft. [120-150 m] el., 11 March 1992 (W.H. Tyson, CDFA), 1 female; E slope of E Butte, 25 March 1992 (W. H. Tyson, CDFA), 1 female; NE slope of W Butte, $36^{\circ} 25^{\prime} 42.5^{\prime \prime} \mathrm{N}, 119^{\circ} 11^{\prime} 52.2^{\prime \prime} \mathrm{W}, 400-500 \mathrm{ft}$. [120-150 m] el., under granite in grassland, 29 March 1991 (D. Ubick, CDU), 6 females; 22 March 2002 (D. and S. Ubick, CDU), 46 females; 9 February 2003 (D. Ubick, W. Savary, CDU, CAS), 1 male, 24 females.

Distribution.- Known only from Tulare County, California (Map 1).

## Genus Cavernocymbium, Ubick, gen. nov.

TyPE SPECIES: Cavernocymbium vetteri, Ubick, sp. nov.
Diagnosis.- Members of this genus can be separated from most cribellate amaurobiids by their small size and pallid, unmarked bodies. The AME are strongly reduced, about $1 / 3$ diameter of the PME, or absent (Fig. 3). Males have strongly modified cymbia with deep internal pockets extending nearly the full length of the cymbium (Figs. 16c-d, 17c-d). Females have epigyna with spirally coiled copulatory ducts (Figs. 12, 14).

Etymology.- The generic name refers to the hollow (caverna, L.) cymbium of the male palp, and is neuter in gender.

Description.- Small cribellate spiders, 1.24-2.60. Color pinkish to white, lacking markings. Carapace piriform in females, subcircular in males (Fig. 2); glabrous with some erect setae on cephalic region. Fovea absent or narrow, longitudinal. Eight or six eyes; AME small, about $1 / 3$ diameter of PME, or absent. Clypeus less than diameter of PLE.

Chelicera with small boss, slightly geniculate in females, with three weak teeth on both margins. Sternum truncate anteriorly, posteriorly extending between coxae IV with extension equal to coxal width; labium pentagonal, less than half length of endites; endites apically converging, ectally rounded, with serrula on anterior margin.

Abdomen with epigastric furrow of male lacking epiandrous spigots. Female with epigynum
a flat plate with paired openings at posterior margin; copulatory ducts in spiral coiling (Figs. 12, 14). Spinnerets with divided cribellum, non-functional in male; ALS largest, twice diameter of PLS; ALS with 2-3 piriform spigots and 1 major ampullate (in female); PMS with 1-2 aciniform spigots, 1 cylindrical spigot (in female), and 1 paracribellar spigot (in female); PLS with 1-2 aciniform spigots, 1 cylindrical spigot (in female), and 3 paracribellar spigots (in female).

Legs lacking spines, or weak spines present on tibiae III, IV p0-0-1. Calamistrum occupying about half length of metarsus IV. Tarsi with 1 or 2 , metatarsi with 2 dorsal trichobothria, distal trichobothria long, bent; trichobothrial base with fine striations as the surrounding cuticle (Fig. 8d-e); tarsi with three claws. Leg formula 1423 (in male) or 4123 (in female).

Male palpus lacking tarsal trichobothria; cymbium large, with deep retrolateral pocket; tibia with ventral, dorsal, and 3-pronged retrolateral apophyses; bulb with long, threadlike embolus, complex conductor, and median apophysis; lacking extra tegular process.

Included species.- Cavernocymbium vetteri and C. pretoglei.
Distribution.- The Mojave region of southern California (Map 1).

## Cavernocymbium vetteri, Ubick, sp. nov.

Figs. 2, 3a, 8d, 11-12, 16; Map 1.
Type material.- Holotype male and allotype female from Mojave Desert Sweeney Granite Mountain Desert Research Center, 8 mi N Hwy 40 on Kelbaker Rd, $34^{\circ} 48^{\prime} 32^{\prime \prime} \mathrm{N}, 115^{\circ} 37^{\prime} 59^{\prime \prime}$ W, San Bernardino County, California, collected at 1220 m in oak (Quercus chrysolepis) leaf duff on 18 May 2001 by R. Vetter; deposited at CAS, courtesy of R. Vetter.

Etymology.- This species is named for Rick Vetter, who spent many hours searching for and rearing these remarkable spiders.

Diagnosis.- This species differs from C. prentoglei by its slightly larger size and the presence of AME (Fig. 3a). Further differences are in the genitalia: the male has a bean-shaped (as opposed to crescent-shaped) cymbium with external undulations (Fig. 16) and the female has longitudinally (as opposed to spherically) coiled copulatory ducts (Fig. 12).

Description.- Male (holotype, range of other males in parentheses; $\mathrm{N}=3$ ): Total length 2.32 (2.14-2.60). Carapace length 0.82 ( $0.80-0.98$ ), width 0.68 ( $0.64-8.84$ ); clypeus length 0.04 . Sternum length 0.55 , width 0.40 ; labium length 0.08 , endite length 0.20 . Abdomen length 1.32 , width 0.80 . Eye sizes and interdistances: AME 0.015, ALE 0.04, PME 0.04, PLE 0.04; AMEAME 0.015, AME—ALE 0.015, PME—PME 0.04, PME—PLE 0.02, ALE—PLE 0.02; PER 0.18, OAL 0.10. Appendages: palp—1.06 ( $0.32,0.24,0,0.60$ ); leg I—2.40 ( $0.70,0.90,0.46,0.34$ ); leg II-2.02 ( $0.62,0.70,0.40,0.30$ ); leg III-1.70 ( $0.52,0.58,0.34,0.26$ ); leg IV—2.32 (0.70, 0.82, $0.48,0.32$ ); leg formula 1423 .

Color: uniformly yellowish white, without markings except for black pigment within eye group. Vestiture: body and legs with dense coat of hairs, sparser on carapace.

Carapace circular in dorsal view, domed (Fig. 2a); fovea absent externally, apodeme visible through carapace; AME smallest, about $1 / 3$ diameter of other, subequal eyes; both rows procurved. Chelicerae narrow, not geniculate, with boss, retromargin with 3 small teeth, promargin with 3 teeth, basal one smallest.

Abdomen with epigastric furrow lacking epiandrous spigots. Spinnerets with non-functional oval cribellum; ALS largest, separated by about one radius; PMS tiny; PLS about as long as ALS, $2 / 3$ width of ALS; ALS with 3 piriform spigots and 3 nubbins; PMS with 2 aciniform spigots and 1 nubbin; PLS with 2 aciniform spigots and 4 nubbins.

Tarsi and metatarsi each with 2 dorsal trichobothria (only one on posterior tarsi), apical longer,
bent; trichobothrial base with fine striations (Fig. 8d); metatarsus IV with vestigial calamistrum represented by curved setae in posterior half.

Palpus large, complex; cymbium lacking trichobothria, bean-shaped with transverse groove, retrolateral and apical margins with cavity containing convoluted passageway; bulb with articulating hook-shaped median apophysis, complex apically-hyaline conductor, lacking additional tegular process; embolus threadlike, arising at base of bulb, curving around bulb (Fig. 16). Tibia with 3-pronged retrolateral apophysis: lateral prongs small, mesal large, apparently flexibly attached (Fig. 11).

Female (allotype, range of other females in parentheses; $\mathrm{N}=6$ ): Total length 2.00 (1.52-2.46). Carapace length $0.80(0.69-0.85)$, width 0.66 ( $0.50-0.66$ ); clypeus length 0.04 . Sternum length 0.54 , width 0.45 ; labium length 0.11 , endite length 0.21 . Abdomen length 1.30 , width 0.88 . Eye sizes and interdistances: AME 0.01 , ALE 0.05 , PME 0.06, PLE 0.07; AME—AME 0.005, AMEALE 0.018, PME—PME 0.05, PME—PLE 0.04, ALE—PLE 0.04; PER 0.27, OAL 0.13. Appendages: palp- 0.88 ( $0.28,0.32,0,0.28$ ); leg I—2.06 ( $0.64,0.80,0.34,0.28$ ); leg II—1.84 ( $0.60,0.64,0.34,0.26$ ); leg III—1.52 ( $0.46,0.52,0.32,0.22$ ); leg IV—2.14 ( $0.66,0.80,0.44,0.24$ ); leg formula 4123.

Color as in male. Carapace piriform in dorsal view (Fig. 2b). Eyes as in male. Chelicerae slightly geniculate, with boss, retromargin with 3 small teeth, promargin with 3 teeth, basal smallest.

Spinnerets with divided cribellum; ALS largest, separated by about one radius; PMS tiny; PLS about as long as ALS; ALS with 3 piriform spigots, 1 major ampullate spigot, and 2 nubbins; PMS with 1 aciniform, 1 cylindrical, and 1 paracribellar spigots; PLS with 2 aciniform, 1 cylindrical, 3 paracribellar spigots and 1 nubbin.

Epigynum flat, with pair of posterior copulatory openings; vulva with longitudinally coiled ducts, diverging anteriorly (Fig. 12).

Metatarsus IV with dorsal calamistrum occupying slightly more than $1 / 2$ length of segment.
Biology.-Specimens were collected from a variety of leaf litter, especially Quercus chrysolepis, but also Acacia greggii, Prunus fasciculate, and Rhus trilobata. In captivity, spiders fed on Collembola.

Other material examined.- Paratypes: CALIFORNIA: San Bernardino Co.: Mojave Desert Sweeney Granite Mountain Desert Research Center: 8 mi N Hwy 40 on Kelbaker Rd, $34^{\circ} 48^{\prime} 32^{\prime \prime} \mathrm{N}$, $115^{\circ} 37^{\prime} 59^{\prime \prime} \mathrm{W}, 1220 \mathrm{~m}$, in oak (Quercus chrysolepis) leaf duff, 18 May 2001 (R. Vetter, UCR), 1 male, 1 female, 1 juvenile; Granite Cove, 5 mi N Hwy 40 on Kelbaker Rd, 4400 ft . [1340 m], in Acacia greggii leaf duff, 26-27 September 1998 (G. Bellmer, UCR), 1 male, 2 female; Prunus fasciculate leaf duff, no date (G. Bellmer, UCR), 1 female; Granite Cove by Pinyon Camp, in pine and squawbush (Rhus trilobata) leaf duff, 1 November 2001 (R. Vetter, UCR), 1 female; Snake Springs, 4010 ft. [ 1220 m ], in oak (Quercus chrysolepis) leaf duff, 1 November 2001 (R. Vetter, UCR) 3 females.

Distribution.- Known only from Granite Mountain, San Bernardino County, California.

## Cavernocymbium prentoglei, Ubick, sp. nov.

Figs. 3b, 6, 8e, 13-14, 17; Map 1.
Type material.- Male holotype from Double Butte, 1 mi NW of Winchester ( 1680 ft . [510 m ] el.), Riverside Co., California, collected in pitfall trap on N -facing hillside of coastal sage scrub on 28 October 2000 by W.R. Icenogle; female allotype, same data except collected under rock on 13 January 1974; deposited at CAS, courtesy of W. Icenogle.

Etymology.- This specific name honors Wendell Icenogle and Tom Prentice who collected most of these unusual spiders.

Diagnosis.- This species differs from $C$. vetteri by its slightly smaller size and the absence
of AME (Fig. 3b). Further differences are in the genitalia: the male has a crescent-shaped (as opposed bean-shaped) cymbium with a basal paracymbium (Figs. 13, 17) and the female has spherically (as opposed to longitudinally) coiled copulatory ducts (Fig. 14).

Description.- Male (holotype, range of other males in parentheses; $\mathrm{N}=9$ ): Total length 1.24 (1.24-1.58). Carapace length $0.54(0.52-0.73)$, width 0.46 ( $0.45-0.55$ ); clypeus length 0.015 . Sternum length 0.35 , width 0.28 ; labium length 0.06 , endite length 0.13 . Abdomen length 0.70 , width 0.44 . Eye sizes and interdistances: AME 0, ALE 0.04, PME 0.04, PLE 0.04; ALE-ALE 0.015, PME—PME 0.02, PME—PLE 0.01, ALE—PLE 0.01; PER 0.15, OAL 0.09. Appendages: palp- $0.68(0.20,0.16,0,0.32)$; leg I— $1.48(0.46,0.54,0.28,0.20)$; leg II— $1.16(0.36,0.40,0.22$, 0.18 ); leg III— 0.94 ( $0.26,0.30,0.22,0.16$ ); leg IV— $1.34(0.38,0.46,0.30,0.20)$; leg formula 1423.

Color: uniformly yellowish white, without markings, carapace slightly darker, palpi dark brown. Vestiture: body and legs with dense coat of hairs, sparser on carapace.

Carapace subcircular in dorsal view, domed; fovea shallow, about $1 / 2$ width of eye region; AME absent, others subequal; PER procurved.

Chelicerae narrow, not geniculate, with small boss, margins with three small teeth.
Abdomen with epigastric furrow lacking epiandrous spigots. Spinnerets with non-functional oval cribellum; ALS largest, separated by about one radius; PMS tiny; ALS longer, stouter than PLS. ALS with 2 piriform spigots and 3 nubbins; PMS with 1 aciniform spigot and 1 nubbin; PLS with 2 aciniform spigots and 2 nubbins.

Tarsi with 1 dorsal trichobothrium, metatarsi with 2, apical longest, bent; trichobothrial base with fine striations (Fig. 8e); metatarsus IV with vestigial calamistrum represented by curved setae in posterior half.

Palpus large, complex; cymbium lacking trichobothria, crescent-shaped, with bilobed basal paracymbium and retrolateral groove forming deep cavity; bulb with articulating sausage-shaped median apophysis (when at rest; MA hook-shaped in expanded palp), apical membraneous conductor, lacking additional tegular process; embolus threadlike, arising at base of bulb and curving around bulb (Fig. 17). Tibia with 4 apical apophyses; 1 dorsal, which abuts cymbium, and 3 retrolateral, lateral one hooking onto cymbial prong, mesal one appears to be flexibly attached, distally expanded (Fig. 13).

Female (allotype, range of other females in parentheses; $\mathrm{N}=4$ ): Total length 1.66 (1.28-1.70). Carapace length 0.68 ( $0.54-0.68$ ), width $0.44(0.41-0.48)$; clypeus length 0.03 . Sternum length 0.40 , width 0.32 ; labium length 0.08 , endite length 0.18 . Abdomen length 1.04 , width 0.64 . Eye sizes and interdistances: AME 0, ALE 0.03, PME 0.04, PLE 0.04; ALE-ALE 0.02, PME-PME 0.03, PME-PLE 0.01, ALE-PLE 0.02; PER 0.15, OAL 0.09. Appendages: palp-0.62 ( 0.20 , $0.22,0,0.20$ ); leg I-1.58 ( $0.50,0.58,0.30,0.20$ ); leg II—1.28 ( $0.40,0.44,0.26,0.18$ ); leg III— 1.08 ( $0.30,0.38,0.26,0.14$ ); leg IV—1.64 ( $0.50,0.60,0.36,0.18$ ); leg formula 4123.

Color as in male. Carapace piriform in dorsal view, domed; fovea not visible externally. Eyes as in male. Chelicerae slightly geniculate, with boss, retromargin with $2-3$ small teeth, promargin usually with 3 teeth.

Spinnerets with divided cribellum; ALS largest, separated by about one radius; PMS tiny; ALS longer, stouter than PLS. ALS with 3 piriform spigots, 1 major ampullate spigot, and 1 nubbin; PMS with 1 aciniform, 1 cylindrical, and 1 paracribellar spigots; PLS with 1 aciniform, 1 cylindrical, and 3 paracribellar spigots (Fig. 6).

Epigynum flat, with pair of posterior copulatory openings; vulva with spherically coiled contiguous ducts (Fig. 14).

Metatarsus IV with dorsal calamistrum occupying slightly more than $1 / 2$ length of segment.

Biology.- This species lives in coastal scrub biomes, from 450 to 600 m elevation, with a few records from desert scrub. Specimens were collected from beneath rocks, in pitfall traps, and from Neotoma nests. One vial, from Winchester, contains a female with an eggsac that is lenticular, constructed of lacy silk, and with two eggs. The species is active during the winter, with adults collected from October through March and a single record in May.

Observations were made on two living males collected by W. Icenogle. The spiders move with a rapid, jerky gait and resemble ants, with the huge dark palpi contrasting strongly with the pale body and resembling an ant's head and mandibles. Legs I are frequently used as antennae, for groping and feeling much in the same way as in phrurolithines. The spiders are unable to climb the vertical smooth surface of a plastic petri dish. When placed on a moistened paper towel they were observed repeatedly cleaning the ventral surfaces of all tarsi with their mouthparts and presumably ingesting the water. The normal resting position of the embolus, observed in both males, is inside the cymbial pocket. The distal part of the embolus protrudes from the distal cymbial opening and the embolar tip rests on the conductor.

Other material examined.- Paratypes: California: Imperial Co.: Indian Wells, 19 mi SE Glamis, Neotoma nest, 25 March1980 (K. Cooper, UCR), 1 female. Riverside Co.: Cactus City, 10 mi W Chiriaco Summit, 1800 ft [ 550 m ], in pitfall trap, 8 January 2000, 2 males (SEM); 26 February 2000, 1male; 14-15 March 2000, 1 male (R. Vetter, UCR); nr. Canyon Lake area, $\sim 0.5$ mi NE of I-15, Summerhill Preserve, off Scenic Ridge Dr., $33^{\circ} 40^{\prime} 12.4^{\prime \prime} \mathrm{N}, 117^{\circ} 17^{\prime} 48.4^{\prime \prime} \mathrm{W}$, el. 1477 ft [ 450 m ], collected in pitfall trap, coastal sage scrub habitat, 10-17 May 2003, 1 female (S. Kirshtner, CTP, UCR); Double Butte, 1 mi NW Winchester, N33 $3^{\circ} 42^{\prime} 58^{\prime \prime}$, W117 $05^{\prime} 33^{\prime \prime}$, el. 1600-1680 ft. [ $490-512 \mathrm{~m}$ ], mostly from pitfall traps on N facing slope near rocky area in coastal sage scrub; 25 January 1975 (in Eriogonum and weed grass litter), 1 female; 24 December 1975 (in debris under rock; gravid, laid eggs before 11 Jan 1976), 1 female with eggsac; 21-23 November 1997, 4 males, 1 female; 21 November 1998, 1 male; 10 November 1999, 3 males; 16 November 2002, 1 male; 28 November 2002, 2 live males; under rock, 7 Mar. 1970, 1 female; 13 March 1976, 1 female (SEM), 1 juvenile (all W. Icenogle, CWI, CAS); between Estelle Mtn. and Harford Springs, off Lake Mathews Rd. (S side), 2.2 mi W of junction Lake Mathews and Gavilan Rds. ( 2.8 mi S of Cajalco Rd.), $33^{\circ} 47^{\prime} 18.3^{\prime \prime} \mathrm{N}$, $117^{\circ} 24^{\prime} 40.3^{\prime \prime} \mathrm{W}$, el. $1960 \mathrm{ft}[600 \mathrm{~m}$ ], pitfall trap, coastal sage scrub habitat, 8-11 November 2003 (S. Kirshtner, CTP, UCR), 5 males; Kabian Co. Park, N of Quail Valley between Canyon Lake and Goetz Road, $33^{\circ} 43^{\prime} 31^{\prime \prime} \mathrm{N}$, $117^{\circ} 14^{\prime} 39^{\prime \prime} \mathrm{W}$, el. 1620 ft [ 490 m ], pitfall trap in coastal sage scrub veg., $11-18$ November 2003 (S. Kirshtner, T.R. Prentice, UCR), 1 male; $33^{\circ} 42^{\prime} 51^{\prime \prime} \mathrm{N}, 117^{\circ} 14^{\prime} 45^{\prime \prime} \mathrm{W}$, el. $1621 \mathrm{ft}[490 \mathrm{~m}], 11-18$ November 2003 (S. Kirshtner, T.R. Prentice, UCR), 1 male; $33^{\circ} 43^{\prime} 30^{\prime \prime} \mathrm{N}, 117^{\circ} 14^{\prime} 43^{\prime \prime} \mathrm{W}$, el. 1580 ft [ 480 m ], $11-18$ November 2003 (S. Kirshtner, T.R. Prentice, UCR), 2 males; $33^{\circ} 43^{\prime} 33.7^{\prime \prime} \mathrm{N}, 117^{\circ} 14^{\prime} 39.6^{\prime \prime} \mathrm{W}$, el. $1670 \mathrm{ft}[570 \mathrm{~m}], 11-18$ November 2003 (S. Kirshtner, T.R. Prentice, UCR), 1 male; $33^{\circ} 43^{\prime} 03^{\prime \prime N}$ N, $117^{\circ} 14^{\prime} 43^{\prime \prime}$ W, el. $1687 \mathrm{ft}[513 \mathrm{~m}$ ], 11-18 November 2003 (S. Kirshtner, T.R. Prentice, UCR), 3 males; Kabian Park, between Canyon Lake and Perris, off Goetz Rd. 3.8 mi S of Case and Goetz Rds. junction in Perris, $33^{\circ} 43^{\prime} 34.0^{\prime \prime} \mathrm{N}, 117^{\circ} 14^{\prime} 38.0^{\prime \prime} \mathrm{W}$, el. $1665 \mathrm{ft}[500 \mathrm{~m}$ ], collected in pitfall trap, coastal sage scrub habitat, 8-11 November 2003 (S. Kirshtner, CTP, UCR), 1 male. Kabian Park, $33^{\circ} 43^{\prime} 29.3^{\prime \prime} \mathrm{N}, 117^{\circ} 14^{\prime} 40.3^{\prime \prime} \mathrm{W}$, el. 1662 ft [ 500 m ], collected in pitfall trap, coastal sage scrub habitat, 10-17 May 2003 (S. Kirshtner, CTP, UCR), 1 female; Lake Perris, hills to the S of lake, W of Mt. Russell, SSW of S end of Redlands Blvd., $33^{\circ} 53^{\prime} 53^{\prime \prime N}$, $117^{\circ} 09^{\prime} 34^{\prime \prime} \mathrm{W}$, el. $2139 \mathrm{ft}[650 \mathrm{~m}]$, pitfall trap, coastal sage scrub veg., 11-18 November 2003 (S. Kirshtner, T. R. Prentice, UCR), 1 male, 1 female; Lake Skinner, "U12 \#7 (m), (m, f) collected together in Winchester and at L. Skinner ARA 449" December 1997 (T. R. Prentice, UCR), 1 male, 2 female; U12 \#3 pitfall trap, 28 November 1998 (T. R. Prentice, UCR), 1 male; B12 \#3 pitfall trap, 20 December 1998 (T.R. Prentice, UCR), 1 male; U12 \#6 pitfall trap, 20 December 1998 (T.R. Prentice, UCR), 1 male; Motte Rimrock Reserve, N of Perris, W of I-215, off W end of Orange Ave., $33^{\circ} 48^{\prime} 46^{\prime \prime} \mathrm{N}, 117^{\circ} 15^{\prime} 18.9^{\prime \prime} \mathrm{W}$, el. $1910 \mathrm{ft}[580 \mathrm{~m}]$, pitfall trap in coastal sage scrub veg., $11-18$ November 2003 (S. Kirshtner, T.R. Prentice, UCR), 1 male; $33^{\circ} 48^{\prime} 40^{\prime \prime} \mathrm{N}, 117^{\circ} 14^{\prime} 52^{\prime \prime} \mathrm{W}$, el. 1630 ft [ 495 m ], 11-18 November 2003 (S. Kirshtner, T.R. Prentice, UCR), 1 male; Multispecies Reserve (SRCMR) Lake Skinner, $33^{\circ} 36.341^{\prime} \mathrm{N}$, $117^{\circ} 01.866^{\prime} \mathrm{W}$, el. 512 m , pitfall trap, 10-13 March 1997 (T.R. Prentice, UCR), 1 female; Shipley Reserve portion N of lake, Lopez Canyon, $33^{\circ} 37^{\prime} 59^{\prime \prime} \mathrm{N}, 11^{\circ} 00^{\prime} 17^{\prime \prime} \mathrm{W}$, Elevation $2230 \mathrm{ft}[680 \mathrm{~m}]$, pit-
fall trap, 13-16 January 2002 (T.R. Prentice, UCR), 1 female; P.L. Boyd Desert Research Center, S Palm Desert, Coyote Creek, pack rat nest, 7 December 1977 (K.W. Cooper, CWI), 1 female.

DIStribution.- Known from Riverside and Imperial counties in California (Map 1).

## Discussion

## Genera

That these spiders are new at the generic level is quite apparent, given their unusual morphology. What may be debated, however, is the number of genera they actually represent. On one hand, the three species may be united into a single genus, as they are somatically similar in spinneret morphology and in having spineless legs and reduced AME. In addition to having strongly modified cymbia, the male genitalia of all three species have an RTA composed of three parts, with a mesal prong apparently flexibly attached to the tibia (Figs. 9, 11, 13). The bulb of each has a complex conductor, with a sclerotized base and trough-like hyaline tip, a large median apophysis, and a threadlike embolus originating basally on the bulb (Figs. 15-17). The females are likewise similar in having genitalia with prominently coiled copulatory ducts (Figs. 10, 12, 14). Alternately, it could be argued that three genera are here represented, as the species show striking differences in genitalic detail. Males differ dramatically in cymbial shape and the form of the retrolateral grooves; females differ in the degree and form of the duct coiling. Here, a middle ground is taken by recognizing two genera: 1) Parazanomys, characterized by a pigmented body, small AME, male cymbium angular with shallow furrow, conductor with large dorsal process, and an additional tegular process (Fig. 15), and females with copulatory ducts arranged in transverse switchback coiling (Fig. 10); and 2) Cavernocymbium, characterized by an unpigmented body, AME tiny or absent, male cymbium with a deep cymbial pocket, bulb lacking enlarged conductor process or an additional tegular process (Fig. 16-17), and females with copulatory ducts with spiral coiling (Figs. 12, 14).

## Family placement

Although most small cribellate spiders in the Nearctic region are placed in Dictynidae, Parazanomys and Cavernocymbium clearly do not belong there. Unlike most dictynids, these spiders have divided cribella and tarsal trichobothria. Dictynids are also defined by a highly derived tracheal system that lacks lateral trunks but has strongly branched median trunks that penetrate the cephalothorax. In Parazanomys, at least, the tracheal system has lateral trunks and only moderately branched median trunks that are restricted to the abdomen (Fig. 4). More significantly, the male genitalia are also not dictynid-like, but have complex tibial apophyses, a median apophysis, and at least a partially hyaline conductor, all characteristic of Amaurobiidae (Griswold et al. 1999).

A search among the Nearctic amaurobiids has turned up a potential sister taxon in the genus Zanomys. These small cribellates are somatically quite similar to Parazanomys in body markings, degree of reduction of the AME, the sculpturing of the trichobothrial hood (Fig. 8b), and in the form of the spinnerets and arrangement of spigots (Fig. 7). Perhaps more significantly, Zanomys males do indeed have what appears to be a short retrolateral furrow on the cymbium (Fig. 18b, d), first noted by Lehtinen (1967) but interpreted by him as a pair of basal ridges. Also, Zanomys shares with the new genera a complex RTA, although one bearing only two prongs, a simple unbranched DTA, a thin embolus in at least some species, and an absence of cymbial trichobothria (Fig. 18). Additionally, the three genera seem to be united by a potential synapomorphy, a sexually dimorphic carapace that is subcircular in males, piriform in females (Fig. 5). On the basis of
these characters, the three genera appear to constitute a clade, here referred to as the "zanomyine complex."

## Subfamily

The Amaurobiidae has seen, in recent years, a steady erosion of its once many subfamilies. Of the nine recognized by Lehtinen (1967), most have now been elevated to family or transferred elsewhere, leaving only Amaurobiinae and Macrobuninae. To these Leech (1972) added Arctobiinae for the monotypic Arctobius Lehtinen 1967. More recently, Wunderlich (1986) included the Agelenidae in Amaurobiidae, of which only the Coelotinae still remain.

A relationship between Zanomys and Arctobius has never been suggested, and the two genera are indeed quite different in both somatic and genitalic features. Leech (1972), on the other hand, considered Zanomys very closely related to Amaurobius C.L. Koch 1837, suggesting even that the two be merged (he retained Zanomys strictly on the basis of its small size). Closer examination, however, indicates numerous genitalic differences between the two. For example, although the male palp of Amaurobius has a retrolateral cymbial modification, it is merely a declivity and not a furrow (Fig. 19d). The palp furthermore differs from Zanomys in having a simple RTA, branched DTA, broad embolus, simple hyaline conductor, and a series of cymbial trichobothria (Fig. 19). Thus, a close relationship between Zanomys and Amaurobius and, by extension, the placement of the zanomyines in Amaurobiinae, seems unjustified.

Lehtinen's (1967) placement of Zanomys in Macrobuninae appears more reasonable, as Macrobunus Tullgren 1901 also has a male palp with a complex RTA and a simple DTA. This genus further resembles Parazanomys and Cavernocymbium in having a flexibly attached tibial apophysis. However, in the latter two genera, the apophysis is the mesal prong of the RTA, whereas in Macrobunus it is the DTA, and so the two states do not seem to be homologous. The macrobunines also have an unusual stridulatory mechanism, consisting of a modified RTA prong and a file on the cymbium, which is absent from the zanomyines. These and other characters (Griswold et. al in press) are believed to support the Macrobuninae as a clade of both cribellate and ecribellate spider genera from the southern hemisphere, and thus exclude the zanomyine complex.

This leaves only Coelotinae, a large Holarctic group of some 20 genera.
One of the chief defining characters for the Coelotinae is a cymbial furrow, first recognized as such by Lehtinen (1967) and substantiated by the phylogenetic analysis of Wang (2002). The zanomyine genera all have structures that could be interpreted as cymbial furrows. In Zanomys, these may be quite short and in Cavernocymbium they form deep pockets. However, in Parazanomys, they are unmistakably coelotine-like. In fact, the similarity between the palpi of Parazanomys and Draconarius aspinatus (Wang et al. 1990) is remarkable and leaves little doubt that the two are closely related (Fig. 20). In both, the cymbium is angular in shape, with a retroapical expansion, and has a long retrolateral furrow enclosing a glabrous region, the embolus is long and thin and originates posteriorly on the bulb, and the conductor is complex with three extensions: a hyaline trough, a dorsal process and a basal lamella. Additionally, females of both have the copulatory ducts (referred to as spermathecae by Wang 2002) arranged in loose coils (see Wang 2002, fig. 193) and males lack cymbial trichobothria [although these were recently detected in some species of Draconarius (Wang 2003)]. Thus, of the various amaurobiid subfamilies, Coelotinae is the best option for zanomyines.

Of course, as coelotines are currently represented only by ecribellates, there may be some reservations to the inclusion of cribellate taxa. However, including the cribellate zanomyines in the subfamily does not pose a problem on logical grounds as numerous instances of closely related cribellate and ecribellate spiders have been documented by, and subsequent to, the pivotal work of

Lehtinen (1967). There are of course some additional differences between the two taxa. Most coelotines have elongated spinnerets, especially the PLS, which are relatively short and compact in zanomyines. Additionally, the genitalia of most coelotines have teeth on the epigynum and a patellar apophysis on the male palp, both lacking in zanomyines. However, these differences appear relatively minor when compared to the potential synapomorphies in genitalic characters, especially as exemplified in Parazanomys and Draconarius.

## Intrasubfamilial relationships

Although it is beyond the scope of this study to conduct a full analysis of coelotine intrarelationships, some observations and predictions can nonetheless be presented.

First, the inclusion of cribellate taxa in the subfamily suggests an obvious value for phylogenetic analysis. In his thorough study of the subfamily, Wang (2002) used the amaurobiid genera, Amaurobius and Tamgrinia Lehtinen 1967, as outgroups and derived a cladogram with Draconarius and relatives occupying the most apical branch. To achieve this, he regarded as derived within the subfamily the following character states: a small epigynal atrium (Wang's character \#6), the presence of a lateral tibial apophysis (\#16) [which is here referred to as a lateral prong of the RTA], a long cymbial furrow (\#20), large conductor lamella (\#23), the presence of a conductor dorsal apophysis (\#24), the posterior origin of the embolus (\#25), an extremely long embolus (\#26), and the presence of a median apophysis (\#28). The fact that these states are also found in Parazanomys and Cavernocymbium brings up interesting possibilities. One is that the states are independently derived in the two groups. However, given the large number of characters involved, this seems unlikely. A second possibility is that these are synapomorphies for the Draconarius group plus the cribellate genera. This interpretation, however, requires either the loss and subsequent appearance of the cribellum, which is generally regarded as most improbable, or the independent loss of the cribellum in each of 11 basalmost taxa of Wang's cladogram (Wang 2002, fig. 56), which would dramatically increase the tree length. The third, and final, possibility is that these character states are synapomorphies at the subfamily level. In other words, the presence of these states in cribellate taxa argues for their plesiomorphy within the Coelotinae and suggests that the Draconarius branch contains the basalmost ecribellate coelotines, and not the apicalmost as hypothesized by Wang.

Perhaps some evidence can be derived from further study of Zanomys, whose genitalia are not of the Draconarius-Parazanomys type. The Zanomys palp, by contrast, is less complex, having a short cymbial furrow and a relatively stout embolus with a more distal origin (Fig. 18). Perhaps this condition is derived, as using Draconarius-Parazanomys as outgroups suggests. On the other hand, this relative simplicity of the Zanomys palp may be primary, suggesting instead the relationship: (Zanomys (Parazanomys (Draconarius (higher coelotines)))). Further study is obviously needed to shed light on these relationships.

## Phylogenetic conclusions

(1) Monophyly of Cavernocymbium. The deep cymbial pockets of the two species appear to be a unique character and a strong synapomorphy for the genus. Additional support is found in the spiral coiling of the female copulatory ducts, the depigmented body, and extreme reduction to loss of the AME.
(2) Parazanomys and Cavernocymbium. The tripartite RTA, and especially the presence of a flexibly attached mesal prong, are interpreted as synapomorphies for these genera. The cymbial furrow in Parazanomys is interpreted as homologous to the cymbial pocket in Cavernocymbium.
(3) Zanomyine complex. Strongest support for this group is the subcircular carapace in males. These species also exhibit a reduction in the AME, but this is also found to some extent in other coelotines and more distant amaurobiids. The distribution of paracribellar spigots in this group, 1 on the PMS and 3 on the PLS, differs from that in Amaurobius, which has 2 on the PMS and 1 on the PLS, and may be of significance. Zanomyines also have a reduced number spigots, which may just be a consequence of their small size: the PLS have 3 or fewer aciniform spigots (at least 5 in Amaurobius and at least 16 in other Coelotinae) (Wang 2002) and the PMS lack minor ampulate spigots [present in Amaurobius and Coelotinae (Wang 2002)]. Also lacking in this group are epiandrous spigots, which are present in Amaurobius and not mentioned by Wang (2002) for Coelotinae. The trichobothrial hood has fine striations, whereas Amaurobius (Fig. 8) and Coelotinae (Wang 2002) have deep transverse grooves.
(4) Zanomyines and ecribellate Coelotinae. Synapomorphies for this group are the cymbial furrow and the complex RTA (bipartite in Zanomys and most Coelotinae, tripartite in Parazanomys and Cavernocymbium), which is derived relative to the single prong in Amaurobius. Zanomyines and Coelotinae also lack trichobothria on the male cymbium, which are present in Amaurobius, but the polarity of this character is not clear.

Ecribellate Coelotinae are derived relative to the zanomyines in lacking a cribellum and having an elongated apical segment of the PLS and in a number of genitalic characters analyzed by Wang (2002), such as the patellar apophysis of the male palpus, a more complex conductor, and female with teeth along the lateral epigynal margin.

## Biogeography

As currently delimited, the subfamily Coelotinae is widely distributed in the Holarctic region, being best represented in east Asia followed by the Mediterranean. The Nearctic fauna is poorly represented, having only two genera, Coras Simon 1898 and Wadotes Chamberlin 1925, which are restricted to the eastern half of the region. With the inclusion of the zanomyine genera in Coelotinae, the geographical gap of western North America is now filled. Although the new genera, Parazanomys and Cavernocymbium, have narrow distributions in southern California, Zanomys extends from southern Canada to Mexico and east to Colorado. Viewed as an area cladogram, the distribution suggests a clear barrier along the Rocky Mountains, separating ecribellate and cribellate coelotines and possibly another in southern California, separating Zanomys from the other zanomyines (Map 2).

## Acknowledgments

Thanks go to: Rick Vetter, Wendell Icenogle, Marge Moody, and Tom Prentice for providing specimens; Suzanne Ubick, Warren Savary, Pierre Paquin, Nadine Dupérré, and Patrick Craig for assistance in the field; Jean Krejca and Joel Despain for helping gain permission for collecting in Sequoia National Park; Warren Savary, Patrick Craig, Saelon Renkes, and Steven Fend for assistance in photography; Charles Griswold, Xinping Wang, Martín Ramírez, and Joel Ledford for stimulating discussions and interpretive help; and Charles Griswold and the Entomology Department at CAS for the use of facilities. Special thanks go to Charles Griswold, Norman Platnick, and Xinping Wang for critically reviewing the manuscript and offering many helpful suggestions.

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## Figures



Figure 1. Parazanomys thyasionnes sp. nov., females from Twin Buttes on undersurface of granite boulders with remnants of webs: a. specimen in light color phase; b. specimen in dark phase (photographs by W. Savary).


Figure 2. Cavernocymbium vetteri sp. nov., carapace, dorsal view: a. male; b. female. Scale bar $=300 \mu \mathrm{~m}$ (a), 270 $\mu \mathrm{m}$ (b).


Figure 3. Cavernocymbium sp., male eye region, dorsal view: a. C. vetteri sp. nov.; b. C. prentoglei sp. nov.. Scale bar $=120 \mu \mathrm{~m}$ (a), $75 \mu \mathrm{~m}$ (b).


Figure 4. Parazanomys thyasionnes sp. nov., female abdomen, ventral, showing tracheal system.


Figure 5. Parazanomys thyasionnes sp. nov., female spinnerets: a. ventral view, b-d. left spinnerets; b. anterior lateral; c. posterior median; d. posterior lateral. $\mathrm{AC}=$ aciniform spigots, $\mathrm{CY}=$ cylindrical spigots, $\mathrm{MAP}=$ major ampullate spigot, $\mathrm{PC}=$ paracribellar spigots, $\mathrm{PI}=$ piriform spigots. Scale bar $=100 \mu \mathrm{~m}(\mathrm{a}), 15 \mu \mathrm{~m}(\mathrm{~b}-\mathrm{c}), 10 \mu \mathrm{~m}(\mathrm{~d})$.


Figure 6. Cavernocymbium prentoglei sp. nov., female spinnerets: a. ventral view; b. anterior lateral spinneret; c. posterior median spinneret; d. posterior lateral spinneret. $\mathrm{AC}=$ aciniform spigots, $\mathrm{CY}=$ cylindrical spigots, MAP $=$ major ampullate spigot, $\mathrm{PC}=$ paracribellar spigots, $\mathrm{PI}=$ piriform spigots. Scale bar $=60 \mu \mathrm{~m}(\mathrm{a}), 8.6 \mu \mathrm{~m}(\mathrm{~b}-\mathrm{d})$.


FIGURE 7. Zanomys californicus (Banks), female spinnerets: a. ventral view; b. anterior lateral spinneret; c. posterior median spinneret; d. posterior lateral spinneret. $\mathrm{AC}=$ aciniform spigots, $\mathrm{CY}=$ cylindrical spigots, $\mathrm{MAP}=$ major ampullate spigot, $\mathrm{PC}=$ paracribellar spigots, $\mathrm{PI}=$ piriform spigots. Scale bar $=120 \mu \mathrm{~m}(\mathrm{a}), 10 \mu \mathrm{~m}(\mathrm{~b}-\mathrm{d})$.


Figure 8. Amaurobiid trichobothria: a. Amaurobius fenestralis Simon; b. Zanomys californicus (Banks); c. Parazanomys thyasionnes sp. nov.; d. Cavernocymbium vetteri sp. nov.; e. Cavernocymbium prentoglei sp. nov. Scale bar $=.7 .5 \mu \mathrm{~m}(\mathrm{a}-\mathrm{b}), 6.0 \mu \mathrm{~m}(\mathrm{c}-\mathrm{e})$.


Figure 9. Parazanomys thyasionnes sp. nov., male palpal tibia: a. retroventral view; b. retrolateral view. $\mathrm{CF}=\mathrm{cym}$ bial furrow, $\mathrm{D}=$ dorsal tibial apophysis, $\mathrm{V}=$ ventral tibial apophysis, $1,2,3=$ prongs of retrolateral tibial apophysis. Scale bar $=350 \mu \mathrm{~m}$.


Figure 10. Parazanomys thyasionnes sp. nov., female genitalia: a. epigynum, ventral view; b. epigynum, lateral view; c. cleared epigynum, ventral view; d. cleared epigynum, dorsal view. Scale bar $=100 \mu \mathrm{~m}$.


Figure 11. Cavernocymbium vetteri sp. nov., male palpal tibia: a. retrolateral view; b. ventral view. V = ventral tibial apophysis, 1, 2, $3=$ retrolateral tibial apophysis prongs. Scale bar $=75 \mu \mathrm{~m}(\mathrm{a}), 100 \mu \mathrm{~m}(\mathrm{~b})$.


Figure 12. Cavernocymbium vetteri sp. nov., female epigynum, cleared: a. ventral view; b. dorsal view. Scale bar = $400 \mu \mathrm{~m}$.


Figure 13. Cavernocymbium prentoglei sp. nov., male palpal tibia: a. retrolateral view; b. retrodorsal view. $\mathrm{CF}=\mathrm{cym}-$ bial furrow, $\mathrm{D}=$ dorsal tibial apophysis, $\mathrm{P}=$ paracymbium, $1,2,3=$ prongs of retrolateral tibial apophysis. Scale bar = 43 $\mu \mathrm{m}$ (a), $60 \mu \mathrm{~m}$ (b).


Figure 14. Cavernocymbium prentoglei sp. nov., female epigynum, cleared: a. ventral view; b. dorsal view. Scale bar $=250 \mu \mathrm{~m}$.


Figure 15. Parazanomys thyasionnes sp. nov., male palp: a. prolateral view; b. ventral view; c. retrolateral view; d. dorsal view. $\mathrm{C}=$ conductor, $\mathrm{CF}=$ cymbial furrow, $\mathrm{E}=$ embolus, $\mathrm{MA}=$ median apophysis, $\mathrm{TP}=$ tegular process. Scale bar $=250 \mu \mathrm{~m}$.


Figure 16. Cavernocymbium vetteri sp. nov., male palp: a. prolateral view; b. ventral view; c. retrolateral view; d. retroventral view. $\mathrm{C}=$ conductor, $\mathrm{CF}=$ cymbial furrow, $\mathrm{E}=$ embolus, $\mathrm{MA}=$ median apophysis. Scale bar $=231 \mu \mathrm{~m}(\mathrm{a}, \mathrm{c})$, $176 \mu \mathrm{~m}$ (b), $136 \mu \mathrm{~m}$ (d).


Figure 17. Cavernocymbium prentoglei sp. nov., male palp: a. prolateral view; b. ventral view; c. retrolateral view; d. dorsal view. $\mathrm{C}=$ conductor, $\mathrm{CF}=$ cymbial furrow, $\mathrm{E}=$ embolus, $\mathrm{MA}=$ median apophysis. Scale $\mathrm{bar}=100 \mu \mathrm{~m}(\mathrm{a}), 120 \mu \mathrm{~m}$ (b-d).


Figure 18. Zanomys californicus (Banks), male palp: a. ventral view; b. retrolateral view; c. apical view of bulb; d. retrolateral view of tibia. $\mathrm{CF}=$ cymbial furrow, $\mathrm{D}=$ dorsal tibial apophysis, $\mathrm{E}=$ embolus, $\mathrm{MA}=$ median apophysis, $1,2=$ retrolateral tibial apophysis prongs. Scale bar $=120 \mu \mathrm{~m}(\mathrm{a}, \mathrm{b}), 60 \mu \mathrm{~m}(\mathrm{c}), 50 \mu \mathrm{~m}$ (d).


Figure 19. Amaurobius fenestralis Simon, male palp: a. ventral view; b. retrolateral view; c. dorsal view of tibia; d. retrolateral view of tibia. $\mathrm{C}=$ conductor, $\mathrm{CD}=$ cymbial declivity, $\mathrm{D}=$ dorsal tibial apophysis, $\mathrm{E}=$ embolus, $\mathrm{MA}=$ median apophysis, $R=$ retrolateral tibial apophysis, $T P=$ tegular process, $T R=$ trichobothria. Scale bar $=430 \mu \mathrm{~m}(\mathrm{a}, \mathrm{b}), 250 \mu \mathrm{~m}$ (c), $176 \mu \mathrm{~m}$ (d).


Figure 20. Male palpi of Parazanomys thyassiones sp. nov. (a, b) and Draconarius aspinatus (Wang et al. 1990) (c, d). a, c. ventral view; b, d. retrolateral view. $\mathrm{C}=$ conductor, $\mathrm{CF}=$ cymbial furrow, $\mathrm{E}=$ embolus, $\mathrm{MA}=$ median apophysis, RTA = retrolateral tibial apophysis.


MAP 1. Southern California showing the distribution of Parazanomys thyassiones sp. nov. (1), Cavernocymbium vetteri sp. nov. (2), and C. prentoglei sp. nov. (3).


MAP 2. Distribution of the Coelotinae. Lines enclose the distribution of the 20 ecribellate genera in the Palearctic and eastern Nearctic (from Wang 2002) and the three cribellate zanomyine genera (z) in the western Nearctic. Darker regions indicate increased generic richness.

