# Taxonomy, phylogeny, and biogeography of the genus *Asydates* Casey (Insecta: Coleoptera: Melyridae)

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**Abstract.** The genus *Asydates* Casey (Coleoptera: Melyridae) is revised, containing three species from Arizona and California: *A. explanatus* Casey; *A. inyoensis* (Blaisdell), new combination; and *A. rufiventris* Casey. The monotypic genus *Pseudasydates* Blaisdell is placed in synonymy with *Asydates* Casey, syn. nov., and *Asydates puncticeps* Blaisdell is placed in synonymy with *Asydates explanatus* Casey, syn. nov. A key separating adults of *Asydates* species is provided, and the results of a computerized cladistic analysis of *Asydates* species are presented. GIS mapping of *Asydates* species distributions indicates that these species are nearly allopatric, with *A. explanatus* found in the lower Colorado River basin and adjacent deserts, *A. inyoensis* restricted to the Inyo and White Mountains, and *A. rufiventris* found in the coastal plain and coastal mountains near Santa Barbara. Geographic hypotheses of character evolution within *Asydates* are developed by combining the results of cladistic analysis and GIS mapping.

## Introduction

The genus *Asydates* Casey (Coleoptera: Melyridae: Dasytinae) contains three species found in southern California and western Arizona. Adults of two species of *Asydates* have been collected on flowers of plant species in the families Cactaceae and Loasaceae, where they may form large feeding aggregations. The dense dorsal setae of adults of *Asydates* species frequently trap pollen grains, which are transported between flowers by adults during the normal course of feeding. It is therefore probable that these beetles are important pollinators of certain plant species. Little else is known about the biology of species of *Asydates*, and the immature stages of these beetles are completely unknown.

The present paper is the first taxonomic revision of *Asydates* since Casey's original treatment of this genus (Casey 1895). The problems in the taxonomy of the genus *Asydates* are typical of taxonomic problems in Nearctic Dasytinae as a whole: both genera and species have been "over-split" by the two previous workers to study this group, T. L. Casey and F. E. Blaisdell. As re-defined here, *Asydates* appears to be a natural group of species within a larger group of genera more or less closely related to *Trichochrous* Motschulsky. A more extensive discussion of the taxonomic relationships of *Asydates* is provided below.

## Materials examined

Adult specimens of species of *Asydates* and allied genera were examined from the collections of the California Academy of Sciences (CASC), the Cornell University Insect Collection (CUIC), and the National Museum of Natural History, Smithsonian Institution (NMNH). As noted below, primary type specimens were examined for *A. explanatus* Casey, *A. puncticeps* Blaisdell, and *A. rufiventris* Casey. Secondary type specimens were examined for these taxa and also for *Pseudasydates inyoensis* Blaisdell. The male holotype of *P. inyoensis* was unavailable for study at the time of this project. It was originally deposited in the California Academy of Sciences, but was sent on loan to an earlier worker who failed to return it to CASC in a timely manner. My conception of this species is therefore based on the female allotype and 28 paratypes of this species that were available for study.

## Genus *Asydates* Casey

*Asydates* Casey (1895:458, 464), Pic (1937:90), Blaisdell (1938:8, 20-21). Type species *Asydates rufiventris* Casey (designated by Blaisdell 1938).

**Synonym:** *Pseudasydates* Blaisdell (1938:8, 18), NEW SYNONYMY. Type species *Pseudasydates inyoensis* Blaisdell (by original designation).

**Diagnosis:** Body relatively large for a dasytine melyrid, length 2.7-4.0 mm, width across humeri 1.0-2.0 mm; antennae serrate, more elongate and slender than in allied genera, reaching at least the middle of pronotum and sometimes the elytral humeri; eyes glabrous; protibia with short spines along dorsal margin; protibial and mesotibial spurs of males spine-shaped, not strongly modified; pronotum more or less strongly shining, disc feebly to moderately densely punctate; pronotum broadest at basal third, lateral margins tapering regularly from basal third to apices; apical angles of pronotum not anteriorly prolonged; lateral portion of pronotal disc not strongly excavate or densely, rugosely punctate; lateral margins of pronotum not strongly serrate; pronotum narrower than elytra at humeri; elytral epipleura broad and planate, flat portion extending at least to apical third or fourth of elytra and sometimes to apices; elytral apices frequently with feeble serrations; elytral pigmentation variable; elytral vestiture variable, comprised either of uniformly reclinate setae or having suberect and/or erect setae interspersed with the reclinate setae; tarsal claws with ventral membranous appendages symmetrical and as long as claws or entirely absent in one species.

**Notes:** Blaisdell (1938) created the genus *Pseudasydates* for a single unusual species that lacked the membranous ventral appendages of the tarsal claws found in most species of Dasytinae. This species, *Pseudasydates inyoensis* Blaisdell, closely resembles *Asydates explanatus* Casey in all of the other character systems that have been used to classify Nearctic genera of Dasytinae by Casey (1895), Blaisdell (1938), and Arnett (1968). It is difficult to find external morphological characters that will consistently and reliably separate adults of *P. inyoensis* and *A. explanatus*, aside from the presence or absence of the tarsal claw appendages. The strong similarity in external adult morphology indicates that *P. inyoensis* is more closely related to *A. explanatus* than either species is to *A. rufiventris*. I therefore interpret the absence of membranous ventral appendages on the tarsal claws of *P. inyoensis* as a secondary loss, and place the genus *Pseudasydates* Blaisdell in synonymy with *Asydates* Casey.

**Discussion of relationships:** As noted above, *Asydates* belongs to a large group of dasytine genera more or less closely allied to *Trichochrous* Motschulsky. Most of these genera are badly in need of species-level revisions, and a number of generic-level synonymies also exist in this group. Within this group, the combination of unmodified male protibial and mesotibial spurs, protibia with short spines along the dorsal margin, pronotum without lateral excavated or rugosely punctate regions, elytral epipleura broad and planate, and ventral membranous appendages present on the tarsal claws and as long as the claws (except in *A. inyoensis*, where these appendages are entirely absent) is diagnostic of adults of *Asydates*. Casey (1895) and Blaisdell (1938) assumed that *Asydates* was closely related to *Eudasytes* Casey, but males of species in *Eudasytes* differ conspicuously from males of species of *Asydates* in having one of the pro- and meso-tibial spurs enlarged and distinctly spatulate. Keys to genera of Nearctic Dasytinae by Blaisdell (1938) and Arnett (1968) will help to separate adults of *Asydates* species from those of allied genera.

## Key to species of *Asydates* Casey

1. Lateral margins of pronotum and elytra with well-defined regular row of fimbriform setae; vestiture of elytral disc uniformly reclinate, without intermingled erect white setae ..... *Asydates rufiventris* Casey
— Setae along lateral margins of pronotum and elytra irregular, not in a row; vestiture of elytral disc irregular and shaggy, erect or suberect white setae present ..... 2

2. Tarsal claws with membranous ventral appendages ..... *Asydates explanatus* Casey
— Tarsal claws lacking membranous ventral appendages ..... *Asydates inyoensis* (Blaisdell)

## *Asydates explanatus* Casey

*Asydates explanatus* Casey (1895:464-466) (HOLOTYPE male, labeled "S California", NMNH type number 37304, examined).

**Synonyms:** *Asydates explanatus* Casey variety *rufipennis* Pic (1910:20); *Asydates puncticeps* Blaisdell (1924:249-250) (HOLOTYPE male, labeled "Potholes Cal./Imperial Co./April 7 1923" and "ex Cactus", CASC type number 1566; five PARATYPES with same data as holotype; one PARATYPE labeled "Potholes Cal./Imperial Co./April 11 1923"; examined), NEW SYNONYMY.

**Illustration:** Grant and Grant (1965:122, Fig. 33E) provide a dorsal habitus illustration of this species, which was misidentified by them as "*Listrus* sp."

**Diagnosis:** Similar to *A. inyoensis* but has membranous ventral appendages on its tarsal claws. Integument dark brownish-black; elytral pigmentation variable, with three common morphs: uniformly yellowish- or reddish-brown; yellowish- or reddish- brown with brownish-black markings along suture and/or at base; or most of disc dark brownish-black with only the apical margin yellowish- or reddish-brown. Elytral vestiture rough, shaggy, comprised of reclinate, suberect, and erect white setae; lateral setae along margins of pronotum and elytra irregular, not forming a fringe of regular, fimbriform setae.

**Notes:** Pic (1910) described *Asydates explanatus* variety *rufipennis* from specimens collected in California. This name was treated as a varietal rather than subspecific name by Pic in his catalogue of world Dasytinae (Pic 1937), and consequently I consider it an infrasubspecific name here. This variety was established by Pic for specimens of *A. explanatus* having the elytra predominantly reddish-brown. Such specimens are found in all populations of this species from which series are available and thus this name is not worthy of recognition even at the subspecific level. *Asydates puncticeps* was described by Blaisdell (1924) from a series of specimens collected on cactus blossoms at Potholes, California. These specimens supposedly differed from *A. explanatus* in having only reclinate setae present on the elytra. However, examination of the holotype, allotype, and five paratypes of *A. puncticeps* reveals the presence of erect or suberect setae on the elytra of all seven specimens. The elytral pigmentation of these specimens is a brighter yellow than that of the type specimens of *A. explanatus*, and the brownish-black pigmentation is reduced in the type specimens of *A. puncticeps* to an indistinct vitta near the suture or an indistinct macula on the base. Examination of series of specimens reveals the presence of many color forms that are intermediate between the elytral pigmentation patterns exhibited by the type specimens of *A. explanatus* (elytral dark brownish-black with lateral and apical margins broadly yellowish) and the pigmentation pattern of the type specimens of *A. puncticeps*. I therefore conclude that only a single, variable species is present.

**Associated plant species:** Adults have been collected on flowers of *Eucnide urens* Parry and *Mentzelia tricuspis* A. Gray (both Loasaceae) and on flowers of unspecified species of Cactaceae.

**Additional specimens examined:** USA: Arizona: Coconino Co., Grand Canyon, ?.VI.? (4, CUIC), Grand Canyon, Bright Angel [Creek], 10.V.1903 (20, NMNH); Mohave Co., 13.7 miles SE Hoover Dam, 20.IV.1967, on *Mentzelia tricuspis* (1, NMNH), 2.8 miles E Willow Beach, 9.IV.1967, on *Mentzelia tricuspis* (1, NMNH), 9.V.1967, on *Mentzelia tricuspis* (1, NMNH), Willow Beach, 19.IV.1967, on *Eucnide urens* (4, NMNH), 2.V.1967, on *Eucnide urens* (4, NMNH), on *Mentzelia tricuspis* (6, NMNH). California: Inyo Co., Panamint Mountains, ?.IV.1891 (1, NMNH); Riverside Co., Palm Springs, edge of Colorado Desert (1, NMNH); San Bernardino Co., 1.7 miles W Parker Dam, 16.IV.1967, on *Eucnide urens* (2, NMNH); San Diego Co., locality not specified, ?.IV.? (15, NMNH); Yuma Co., Yuma, ?.III.1913 (2, NMNH). Question mark (?) indicates data missing on original label.

## *Asydates inyoensis* (Blaisdell) new combination

*Pseudasydates inyoensis* Blaisdell (1938:18-20) (ALLOTYPE female, labeled "Silver Canyon/Cal./May-10-1926" and "White Mtns./Inyo Co.", CASC; 22 PARATYPES with same data as allotype, CASC; 6 PARATYPES labeled "Payson Cn./Cal/May-6-1923" and "White Mtns./Inyo Co.", CASC; examined).

**Diagnosis:** Similar to *A. explanatus* in size and general appearance except that the membranous ventral appendages of the tarsal claws are absent. The elytral color variation in this species parallels that of *A. explanatus*: some specimens are predominantly dark brown with the elytral apices lighter in color, others have the elytra predominantly reddish-brown, while others have the elytra yellowish-brown with a brown or black vitta along the suture which may extend across the elytral bases.

**Associated plant species:** Blaisdell (1938) reports that adults were collected on *Eucnide urens* (Loasaceae) in Mosaic Canyon, Death Valley, California.

**Additional specimens examined:** USA: California: Inyo Co., Panamint Mountains, ?.IV.1891 (12,

**Table 1.** Taxon-character matrix for cladistic analysis of *Asydates* species

| Species | Char. 1 | Char. 2 | Char. 3 | Char. 4 | Char. 5 | Char. 6 | Char. 7 | Char. 8 |
|---|---|---|---|---|---|---|---|---|
| *Trichochrous laticollis* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Eudasytes desertus* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| *Eudasytes hirsutus* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| *Asydates explanatus* | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| *Asydates inyoensis* | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Asydates rufiventris* | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |

NMNH), ?.V.1974 (23, NMNH), Panamint Valley, ?.IV.1891 (21, NMNH). Question mark (?) indicates data missing on original label.

## *Asydates rufiventris* Casey

*Asydates rufiventris* Casey (1895:464-465) (HOLOTYPE female, labeled "Cal", type locality given in description as Santa Barbara, California, NMNH type number 37303; 3 PARATYPES with same data as holotype, examined).

**Diagnosis:** Easily separated from the other species of *Asydates* by its uniform elytral vestiture without intermingled erect setae and by the presence of a fringe of fimbriform setae along the lateral margins of the pronotum and elytra. The elytra are predominantly black in the six specimens examined, with the apical margin narrowly yellowish-brown.

**Additional specimens examined:** USA: California: Kern Co., Tehachapi (2, NMNH).

## Phylogeny of *Asydates*

The following adult morphological characters were used in a cladistic analysis of the species of *Asydates*:

**Character 1:** Antennae: short, seldom attaining midsection of pronotum, segments stout (0); long, easily attaining pronotal midsection, segments more slender (1).

**Character 2:** Protibial and mesotibial spurs in male: one spur modified, curved and spatulate (0); both spurs spine-like (1).

**Character 3:** Membraneous ventral appendages of tarsal claws: present (0), absent (1).

**Character 4:** Pronotum: as broad as elytra or only slightly narrower than elytra (0); distinctly narrower than elytra (1).

**Character 5:** Lateral setae of pronotum: irregular (0); in a single, regular row (1).

**Character 6:** Elytral epipleura: not broadly explanate (0); broadly explanate (1).

**Character 7:** Lateral setae of elytra: irregular (0); in a single, regular row (1).

**Character 8:** Elytral vestiture: reclinate setae only (0); both reclinate and suberect setae present (1).

Three species from related genera, *Trichochrous laticollis* Mannerheim, *Eudasytes desertus* Blaisdell, and *E. hirsutus* Blaisdell, were selected as outgroup taxa to root the most parsimonious network(s) found by cladistic analysis. Paratype specimens of *E. desertus* and *E. hirsutus* and specimens identified as *T. laticollis* by T. L. Casey were examined in the NMNH collection.

A taxon-character matrix (Table 1) was constructed for these five species using the WINCLADA software package (Nixon 1999), and cladistic parsimony analysis of this matrix was performed using the fast parsimony program NONA (Goloboff 1993). A single most parsimonious tree having length 9, consistency index 88, and retention index 90, was recovered from cladistic analysis (Figure 1). Character state changes were mapped to this tree

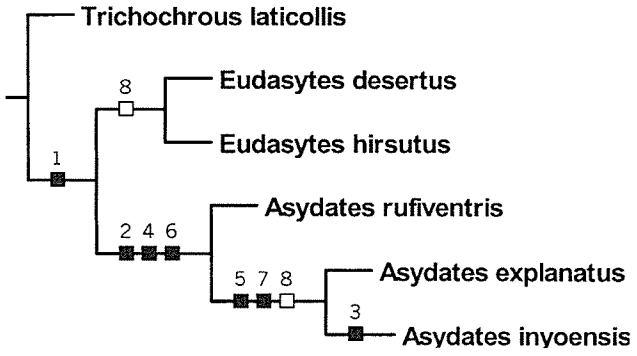


**Figure 1.** Most parsimonious cladogram of *Asydates* species, having length 9, consistency index 88, and retention index 90. Analysis was performed with NONA (Goloboff 1993) and cladograms examined in WINCLADA (Nixon 1999). Characters were optimized to support the monophyly of *Eudasytes*; the only ambiguous optimization is that of character 8. Black squares indicate unambiguous forward steps; white squares indicate homoplastic forward steps.

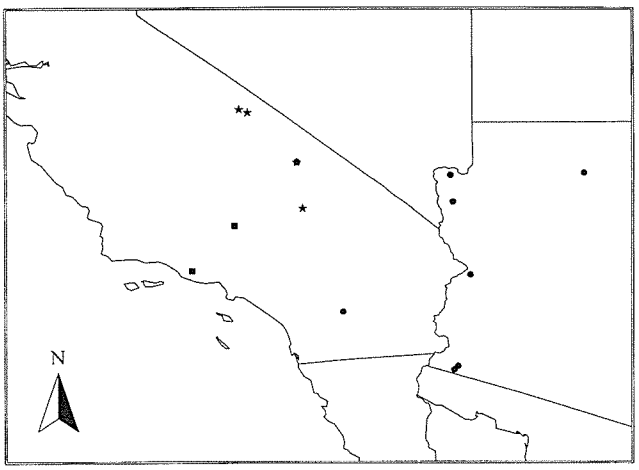


**Figure 2.** Distributions of *Asydates* species, mapped with ArcView GIS software (ESRI 1999). Circles indicate collecting sites for *A. explanatus*, stars indicate collecting sites for *A. inyoensis*, and squares indicate collecting sites for *A. rufiventris*. The one anomalous symbol is a superimposed star and circle.

using the WINCLADA software package. This tree represents the best available hypothesis of phylogenetic relationships for the species of *Asydates*.

## Biogeography of *Asydates*

The latitude and longitude coordinates for sites at which species of *Asydates* were collected were identified using the United States Geological Survey's Geographic Names Information Server, available on the World Wide Web (http://geonames.usgs.gov/pls/gnis/web_query.gnis_web_query_form). The ArcView Geographic Information System (GIS) software package (ESRI 1999) was then used to map these sites on a digital map of the United States and Mexico (Figure 2). Examination of this map shows clearly that the distributions of the three species of *Asydates* are nearly allopatric, with only a small degree of overlap between *A. explanatus* and *A. inyoensis* in the Panamint Mountains. *Asydates explanatus* is found primarily in the lower Colorado River basin and adjacent deserts, *A. inyoensis* is restricted to the Panamint and White Mountains, while *A. rufiventris* occurs in the coastal plain and coastal mountains in the vicinity of Santa Barbara. Comparison of this map with a digital vegetation map of California published by the California Gap Analysis Project (Davis et al. 2000) shows that *A. rufiventris* is associated with coastal chaparral vegetation, while *A. explanatus* and *A. inyoensis* are associated with vegetation of the Mojave desert.

These GIS maps also provides insight into the geographic evolution of individual characters in the genus *Asydates*. The cladogram in Figure 1 suggests that the derived states of characters 5, 7, and 8 (states 0, 0, and 1, respectively) evolved in the most recent common ancestor of *A. explanatus* and *A. inyoensis*, with the primitive state for these characters present in both *A. rufiventris* and the most recent common ancestor of all *Asydates* species. *Asydates explanatus* and *A. inyoensis* are both associated with deserts and desert mountains, while *A. rufiventris* is confined to the more mesic coastal plain and coastal mountains. It could be hypothesized that the evolution of the derived states in characters 5, 7, and 8 was associated with the adaptation of the most recent common ancestor of *A. explanatus* and *A. inyoensis* to desert habitats. These three character changes all involved shifts from regular to irregular elytral and/or pronotal setae. The function of irregular, elongate dorsal and lateral setae in desert species of *Asydates* is not clear, although similar setae are found in desert species of the genera *Trichochrous* Motschulsky (Coleoptera: Melyridae: Dasytinae) and *Cymatodera* Gray (Coleoptera: Cleridae: Tillinae).

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