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A NEW SUBSPECIES OF *OCHLODES YUMA*
(W. H. EDWARDS)
WITH NOTES ON LIFE HISTORY AND
HISTORICAL BIOGEOGRAPHY

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INTRODUCTION

Ochlodes yuma was first described by W. H. Edwards (1873), who listed the type locality as "Arizona." Brown (1957) cogently argued that the type specimens probably were collected along the Owens River Valley in Inyo County, California, and restricted the type locality accordingly. Years later, a similar skipper from western Colorado was given the name *scudderi* by Skinner (1899). Tilden (1957) reviews the taxonomic history of this insect in more detail.

Most modern workers (e.g., Tilden, 1957, 1961; Brown, 1957; Scott et al., 1977; Stanford, 1981; Miller and Brown, 1981; Scott, 1986) consider *scudderi* to be a synonym of *yuma*. These authors judged morphological differences between *scudderi* and *yuma* as inadequate to warrant subspecies status. For example, Scott et al. (1977) noted "some individual variation in the width of the dorsal forewing dark border," but then concluded there was no consistent geographic variation between then-known populations. A recently discovered colony in the state of Washington also is consistent with typical *yuma* (Pelham, 1988b). These similarities across such great distances are more noteworthy because of the frequent occurrence of *yuma* in small, isolated colonies.

On August 12, 1984, *Ochlodes yuma* was observed at the Rio Grande Gorge near the community of Questa, in Taos County, New Mexico (Cary, 1985). Two males and one female were collected in and around a patch of the Common Reed, *Phragmites australis* (Cav.) Trin. exSteud. (Poaceae), growing in a broad seep/spring area at an elevation of about 2070 m near the bottom of the 250 m deep Rio Grande Gorge. The specimens were sent to R. E. Stanford who, in consultation with James A. Scott, examined the genitalia and determined them to be *Ochlodes yuma*.

This colony contrasts with the phenotypic consistency of nominate *O. yuma* across the Great Basin of the western United States. The Taos Co. colony is markedly different from the nominate race in terms of wing maculations and biogeography.

Ochlodes yuma anasazi, new subspecies

Figures **1, 2** ♂, **3, 4** ♀

Diagnosis and Description: The new taxon is so much darker than any other examples of the species that upon first sighting it was thought to be a different species. Careful examination of the type series, including genitalia, and comparison with other specimens revealed that it is indeed *yuma*. A second feature distinguishing *anasazi* from other *yuma* is the series of relatively prominent postdiscal light spots on the ventral hindwing (VHW).

Holotype male (Figs. **1,2**): Forewing length (FWL) 16 mm. Forewing (FW) and hindwing (HW) are dorsally fulvous with prominent marginal dark markings extending inward nearly to the stigma on the FW, with the inner edge diffuse (see Figures **1,2**). The subapical fulvous FW markings are quite conspicuous against this dark background. The dark border along the costa and distal margin of the HW is wider than in any other populations of the species. On the dorsal surface typical *yuma* is fulvous with dark markings, for example in the Washington colony (Pelham, 1988b:5), but *anasazi* is predominately dark with postdiscal fulvous spots. The VFW differs from other *yuma* populations in having a much larger basal black patch. The VHW ground color is greenish
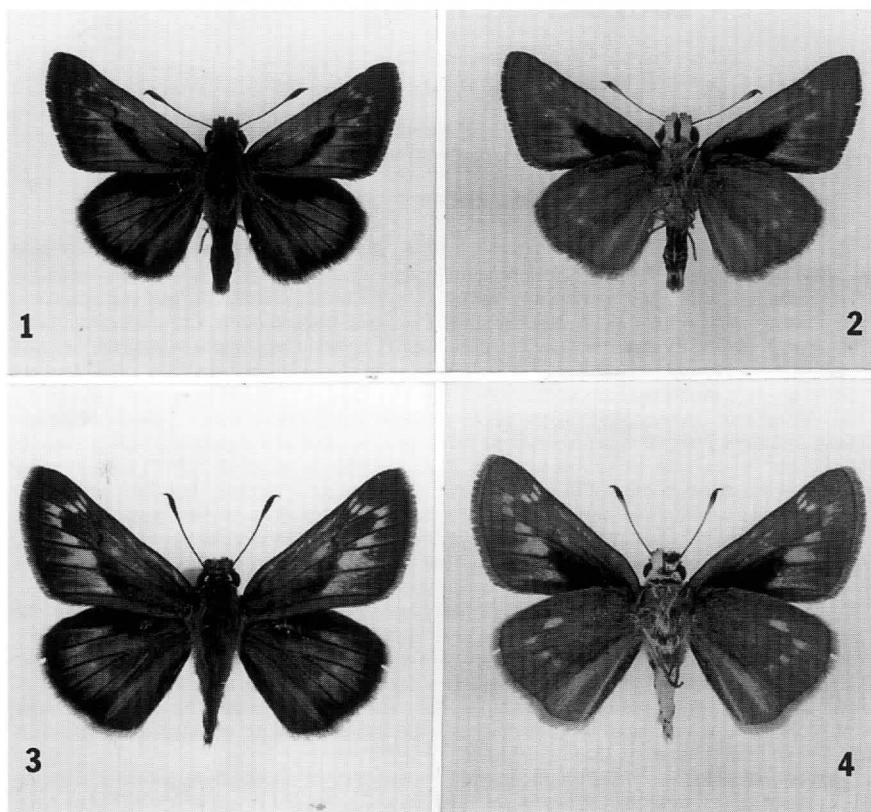
Figures **1-4**. *Ochlodes yuma anasazi*, new subspecies. Holotype male, dorsal (**1**) and ventral views (**2**). Allotype female, dorsal (**3**) and ventral (**4**) views.

yellow and darker than in other populations. The postdiscal series of light yellow spots on the VHW is relatively prominent. These spots are almost inapparent in individuals from other populations because of their lighter ground color (Pelham, 1988b: 5; Stanford, 1981: 107). Characters of the stigma, antennae, palpi and other body parts were examined and found to be not different from other *yuma*. The genitalia also are similar.

Allotype (primary paratype) female (Figs. **3,4**): FWL 18 mm. FW and HW are dorsally fulvous, but marked by black even more than in the male (see Figures **3,4**), almost as dark as female *Poanes taxiles* (W. H. Edwards). In the place of the male stigma is a large dark patch which extends to the dark borders; nominotypical *yuma* females, in contrast, have at most a few dark scales. The dorsal fulvous cast of nominotypical *yuma* females contrasts with the dark appearance of *anasazi* females. As in the male, the subapical fulvous spots are prominent against the darker surroundings. The DHW is alternately light and dark. The VFW is similar to the male. The VHW is darker than that of the male, a medium grey-green with a prominent series of postdiscal pale yellow spots. Characters of the antennae, palpi, and other body parts are not different from other *yuma*.

Type Locality and Types: This distinctive subspecies is described from 35 males and 17 females from the type locality (TL), New Mexico: Taos Co, Rio Grande Gorge near Questa. The holotype male, 8 paratype males, and 7 paratype females are from the TL, 9 August 1986, collected by S. J. Cary. The allotype female, 17 paratype males, and 5 paratype females are from the TL, 17 August 1986, collected by R. E. Stanford. The remaining 9 paratype males and 4 paratype females are from the TL, 15 August 1989, collected by A. D. Warren. This subspecies is known only from the TL.

Disposition of types: The holotype, allotype and two paratype pairs will be deposited in the Allyn Museum of Entomology/Florida Museum of Natural History. Two paratype pairs each will be distributed to the American Museum of Natural History, the National Museum of Natural History/Smithsonian Institution, and the Natural History Museum of Los Angeles County. One paratype pair will be placed in each of the following institutions: University of Colorado Museum, Denver Museum of Natural History, California Academy of Sciences, and Colorado State University. Remaining paratypes will remain in the collections of the authors.

Variation: The specimens examined, while not uniform, are relatively homogeneous. The male paratypes have an average FWL of 16.1 mm (range 15.5-17 mm), while the females average 17.6 mm (range 16-18.5 mm). Some variability is apparent in the width of the dorsal dark borders, as observed by Scott et al. (1977) for other *yuma* populations. However, even the lightest specimen of the New Mexico colony is still much darker than any other *yuma* examined. One male paratype is almost completely dark, resembling no other taxon. Prominence of the ventral postdiscal pale spots also varies, but this may be attributable chiefly to variable wear on individual specimens.

Etymology: The new subspecies is given the name *anasazi*, a reference to the Anasazi Culture which flourished in the Southwest about 500 years ago (Jennings, 1974: 293). The lands of the Anasazi people included much of the Colorado Plateau; the *anasazi* skipper colony is on the eastern margin of this territory. Perhaps best known for spectacular cliff dwellings and multi-story masonry houses such as those at Mesa Verde National Park, Colorado, and Chaco Canyon National Monument, New Mexico, the Anasazi also were agriculturalists skilled at exploiting limited water resources. As water was crucial for the Anasazi people, it also influences the occurrence of *Ochlodes yuma*. The skipper is strictly dependent upon *Phragmites australis*, an emergent aquatic plant which requires the presence of water in the form of rivers, lakes, or springs. *Anasazi* therefore is an appropriate name for this new subspecies of *yuma*.

LIFE HISTORY

Immatures and larval host: Useful life cycle information is provided by Scott, **et al**. (1977), Scott (1986: 505), and Pelham (1988a, 1988b). Larvae have been reared successfully on leaves of the only known larval host plant, *Phragmites australis* (Emmel and Emmel, 1973). Larvae of the *anasazi* colony feed on *australis* foliage at the type

locality. One captive larva fed on *australis* leaves obtained from a different locality. Also known as the Common Reed, *australis* is a tall (2-4 m), sturdy, colonial, annual grass (Gleason and Cronquist, 1963: 66). It is nearly worldwide in distribution and occurs throughout most of North America, preferring wet habitats.

In single-brooded populations of *O. yuma*, first instar larvae hatch in late summer or autumn and enter diapause without feeding (Pelham, 1988b). Feeding begins in spring; individuals of the single-brooded New Mexico colony are in the second instar by mid-May. Early instars make tube shelters by rolling and fastening one edge of an *australis* leaf. By July, *anasazi* larvae are in later instars. Mature larvae make shelters by rolling and fastening both leaf edges together. The final larval instar builds a shelter tube and pupates within it.

Adults: Like most related skippers, *O. yuma* is an active and occasionally speedy flyer. Adults nectar at a variety of flowers, preferring thistles *(Cirsium* spp.) at the New Mexico colony and elsewhere (e.g., Pelham, 1988a). From perches on or near the larval host, males investigate passing objects in search of females. Copulation has been observed in the early afternoon (Scott et al., 1977: 21). Oviposition has been observed in early afternoon on hostplant leaves (Pelham, 1988a) and at the base of the plant (Scott et al., 1977: 21).

Distribution: A map illustrating the current geographic distribution of *yuma* is provided as Figure **5**. Although all colonies cannot be shown at this mapping scale, the dot symbols accurately depict the widespread, yet disjunct nature of colonies. The new subspecies is known only from the Taos Co., New Mexico locality. The larval host is widespread in New Mexico, but large stands are scarce. A few promising areas have been identified in nearby Rio Arriba, Cibola, and Santa Fe counties, but searches there for *yuma* have been futile. The Taos County colony remains the only known colony in New Mexico and the only known colony east of the Continental Divide. It is about 300 km southeast of the nearest known colonies in Colorado, and 500 km east of the nearest known colonies in Arizona and Utah. Among all colonies known to the authors, it is at the highest altitude above sea level.

Voltinism: The Taos County colony is single-brooded; adults fly from late July into early September. Throughout the overall range of *O. yuma*, univoltine populations are found at high latitude (Oregon and Washington) or high altitude (Colorado, New Mexico). Bivoltine populations typically are reported from lower elevations in Nevada, Southern Utah and California. The length of growing season may be an important factor in determining the number of annual broods. In an analogous situation, populations of *Poanes viator zizaniae* Shapiro (Hesperiidae) which utilize *Phragmites australis* along the Atlantic Coastal Plain in eastern North America complete one annual generation in the north, but two or more in the south (Opler and Krizek, 1984: 247).

HISTORICAL BIOGEOGRAPHY

Historical biogeography of *Ochlodes yuma* should be dynamic, and its modern distribution should be complex, because the skipper relies upon an aquatic larval hostplant in a region where wetland habitats have undergone dramatic transformations and translocations caused by Pleistocene and Holocene climate changes (e.g., Shapiro, 1970[1971]). Austin (1985) suggests how principles of island biogeography might apply to riparian organisms in the arid Southwest.

During glacial maxima of the Pleistocene Epoch, southwestern North America was characterized by climates that were moist and less subject to seasonal extremes compared to today. Winter storms coming onshore from the Pacific Ocean were diverted south, routinely passing south of the crest of the Sierra Nevada and delivering abundant moisture to the interior Southwest (Spaulding and Graumlich, 1986: 441-442). Added winter moisture in that region raised ground-water tables, increased numbers and flows of perennial rivers and springs, and created freshwater lakes. These conditions prevailed in now arid basins as recently as 20,000 years ago, and over an area "south of about 35°and from Texas westward" (Smith and Street-Perrott, 1983: 205-208). With the
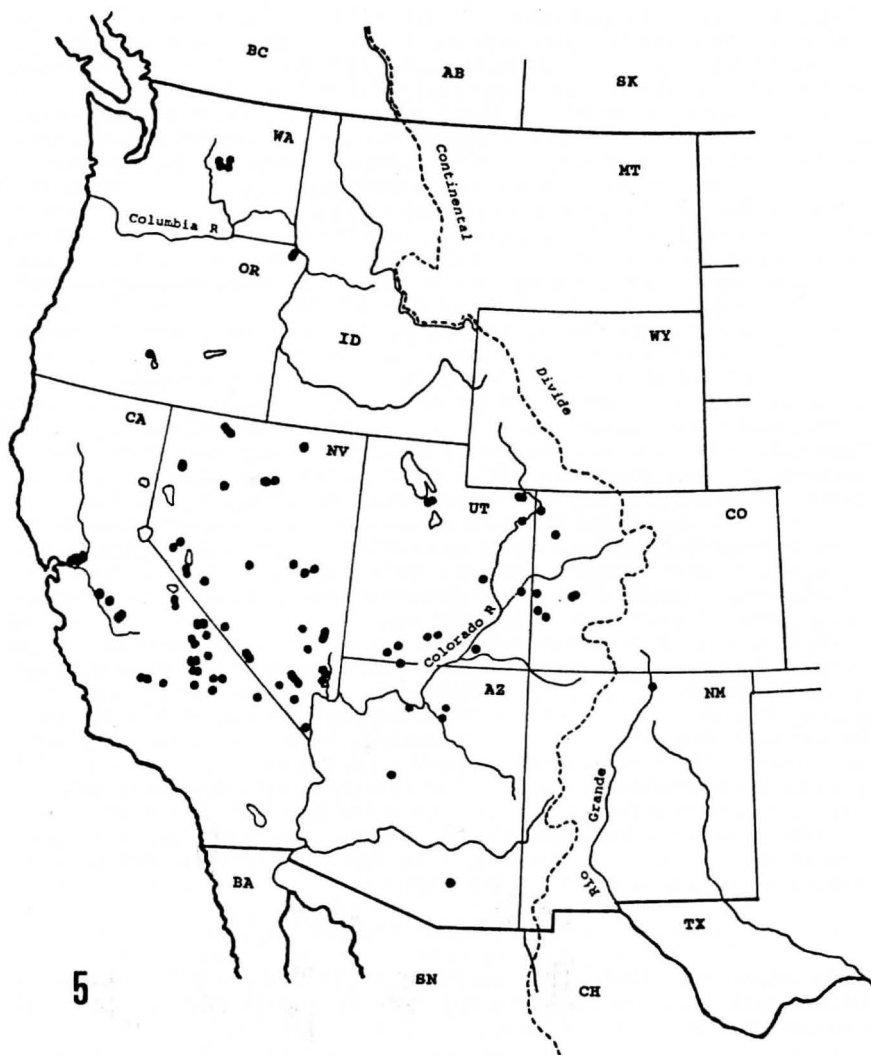
Figure **5**. Distribution of *Ochlodes yuma* in western North America.

assistance of abundant beaver populations, alluvial plains and river valleys in the region were characterized by high water tables, marshy sloughs, backwaters, oxbow lakes, and boggy stream margins (Minckley and Brown, 1982: 225).

Theoretically these conditions should have been favorable for *Phragmites australis*; direct evidence, though scant and local, supports this. For example, Quade (1986: 346) documents expanded "reed-filled" marshes near Las Vegas, Nevada, during this period. Extrapolating, it can be inferred that these conditions were more prevalent throughout the Southwest during the Pleistocene than they are today. These expanded hostplant networks may have supported widespread and freely interbreeding populations of *yuma*

throughout the area of pluvial climate. The Taos County colony of *yuma*, along the Rio Grande, may mark the approximate eastern limit of the Pleistocene range of *yuma*.

Present isolation of *anasazi* in a physiographic cul-de-sac testifies to the impacts that Pleistocene-ending climate change had on water tables, aquatic habitats, *australis*, and *yuma*. Pluvial lakes in Arizona, New Mexico and Texas began declining 13,000 years ago and were dry by 10,000 years ago (Smith and Street-Perrott, 1983: 206-207). As a result, many colonies and corridors of *yuma* probably were eliminated. The Continental Divide, which crosses the affected region, may have emerged early as an effective physiographic barrier and may have contributed to reproductive isolation of eastern *yuma* outposts in New Mexico. Austin (1985) argues that when suitable riparian habitats become separated by great expanses of unsuitable habitat, individual populations become unable to colonize new areas, lose reproductive contact with neighbor colonies, and are prone to extirpation. This scenario may be relevant for *yuma* in the Southwest, particularly in the area east of the Continental Divide. There, along the Rio Grande, the processes of climate change and habitat loss perhaps culminated in *anasazi*.

We concur with Scott et al. (1977) that "current colonies seem to be relicts of a formerly widespread Pleistocene distribution." The former range of *yuma*, and its taxonomy, can better be understood by further examination of the extensive literature concerning Pleistocene and Holocene environments in the region and by application of the reasoning of Austin (1985) and Shapiro (1970[1971]). For example, lack of differentiation between eastern California and western Colorado populations, where original types of *yuma* and *scudderi* were collected, may be related to the absence of any barrier to reproduction along the Colorado River, which loosely connects the two type localities. Even today, in the absence of pluvial conditions, the Colorado River system still hosts scattered *yuma* colonies along its length, affording opportunities for gene flow between even the most distant *yuma* outposts along its far-flung tributaries.

Like *O. y. anasazi*, Washington and Oregon colonies exist far from core *yuma* areas. Notably, Pleistocene conditions favorable to *yuma* south of 35°N latitude did not necessarily extend north into the Great Basin of Nevada. *Ochlodes yuma* may have been excluded from that area by cold temperatures and a short growing season (Spaulding et al., 1984: 24). After Pleistocene weather patterns were supplanted, however, the north/south orientation of many lake-and-marsh-filled valleys of the Great Basin may have promoted northward dispersal of *yuma*. Paleoclimatic evidence therefore suggests that *yuma* populations in Oregon and Washington may be relatively new, probably of Holocene age (<10,000 years). Morphology is consistent with this idea, as specimens from these colonies exhibit little differentiation from typical *yuma* (Pelham, 1988b), suggesting relatively recent connection with core *yuma* areas.

ACKNOWLEDGEMENTS

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Note added in proof:

In 1994, R. Langston located *O. yuma* in the Wind River Canyon in Wyoming. This colony is on the east slope of the Continental Divide, but the phenotype matches nominate *yuma*, not the subspecies, *anasazi*.

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