= Oryzomys couesi =

Oryzomys couesi , also known as Coues ' rice rat , is a semiaquatic rodent in the family Cricetidae occurring from southernmost Texas through Mexico and Central America into northwestern Colombia . It is usually found in wet habitats , such as marshes , but also lives in drier forests and shrublands . Weighing about 43 to 82 g (1 @.@ 5 to 2 @.@ 9 oz) , O. couesi is a medium @-@ sized to large rat . The coarse fur is buff to reddish above and white to buff below . The hindfeet show some specializations for life in the water , such as reduced ungual tufts of hair around the digits . It has 56 chromosomes . There is much geographic variation in size , proportions , color , and skull features . Oryzomys couesi is active during the night and builds nests of vegetation that are suspended among reeds about 1 m (3 @.@ 3 ft) above the ground . It is an excellent swimmer and dives well , but can also climb in vegetation . An omnivore , it eats both plant and animal food , including seeds and insects . It breeds throughout the year ; females give birth to about four young after a pregnancy of 21 to 28 days . The species may be infected by several different parasites and by two hantaviruses .

The species was first described in 1877 , the first of many related species from the region described until the 1910s . In 1918 , Edward Alphonso Goldman consolidated most into the single species Oryzomys couesi and in 1960 Raymond Hall united this taxon with its United States relative , the marsh rice rat (O. palustris) , into a single widespread species ; subsequently , many related , localized species retained by Goldman were also included in this taxon . After studies of the contact zone in Texas , where O. couesi and the marsh rice rat meet , were published in 1979 and underscored the distinctness of the two , they were again regarded as separate . Since then , some of the peripheral forms of the group , such as Oryzomys antillarum from Jamaica and Oryzomys peninsulae from the Baja California Peninsula , have been reinstated as species . Nevertheless , O. couesi as currently constituted is likely a composite of several species ; a 2010 study , using DNA sequence data , found evidence to recognize separate species from the Pacific and eastern sides of the distribution of O. couesi and two additional species from Panama and Costa Rica . Generally , Oryzomys couesi is common and of no conservation concern , and it is even considered a plague species in places , but some populations are threatened .

= = Taxonomy = =

Oryzomys couesi and at least six more narrowly distributed species with peripheral distributions together form the O. couesi group within the genus Oryzomys . The eighth species of the genus , the marsh rice rat (O. palustris) is the only member of its own group (unless western populations are classified as a separate species , O. texensis) . Oryzomys previously included many other species , which were reclassified in various studies culminating in contributions by Marcelo Weksler and coworkers in 2006 that removed more than forty species from the genus . All are placed in the tribe Oryzomyini (" rice rats ") , a diverse assemblage of over a hundred species , and on higher taxonomic levels in the subfamily Sigmodontinae of the family Cricetidae , along with hundreds of other species of mainly small rodents .

= = = History = = =

Edward Alston first described Oryzomys couesi in 1877 , using three specimens from Mexico and Guatemala . He named the animal Hesperomys couesi , placing it in the now @-@ defunct genus Hesperomys , and noted similarities to the marsh rice rat (then called Hesperomys palustris) and two species now placed in Tylomys . The specific name , couesi , honors American naturalist Elliott Coues , who had done much work on North American rodents . In 1893 , Oldfield Thomas wrote that the species , by then placed in the genus Oryzomys as Oryzomys couesi , had caused much confusion about its identity , because the three specimens (one from Cobán , Guatemala , and two from Mexico) used by Alston in fact belonged to two or three different species . He restricted the name couesi to the animal from Guatemala , and introduced the new name Oryzomys fulgens for

one of the Mexican animals . Several other related species were described from the early 1890s onwards and in 1901 Clinton Hart Merriam united many of those into a palustris @-@ mexicanus group of species , which also included the marsh rice rat .

Edward Alphonso Goldman revised North American Oryzomys in 1918 and consolidated many forms into a single species Oryzomys couesi , with ten subspecies distributed from southern Texas and western Mexico south to Costa Rica . He placed it in an Oryzomys palustris group with the marsh rice rat and several species with more limited distributions , which he regarded as related to O. couesi but distinctive enough to be classified as separate species . In the 1930s , a few more forms related to O. couesi were described . As then recognized , the ranges of the marsh rice rat , a United States species , and Oryzomys couesi meet in southern Texas . In 1960 , Raymond Hall reviewed specimens from this contact zone and found no grounds on which to separate the two species ; thus , he reduced O. couesi to a subspecies of the marsh rice rat . Other workers continued this lumping and by 1971 all other species Goldman had placed in the O. palustris group were classified under the marsh rice rat , together with Oryzomys azuerensis from Panama , described as a species in 1937 .

Additional studies of the palustris ? couesi contact zone in Texas published in 1979 , using more specimens and characters , indicated that the two species are in fact easily distinguishable there ; therefore , O. couesi has since been regarded as a species distinct from the marsh rice rat . Afterward , some of the other forms synonymized under O. couesi or O. palustris were resurrected as separate species ? Oryzomys nelsoni from the Marías Islands , western Mexico , and Oryzomys antillarum from Jamaica . In 2009 , Michael Carleton and Joaquin Arroyo @-@ Cabrales reviewed western Mexican Oryzomys , reaffirmed the distinctness of O. nelsoni , and reinstated O. peninsulae from the tip of the Baja California Peninsula and O. albiventer from interior Mexico as species . Still , O. couesi included 22 synonyms , and Carleton and Arroyo @-@ Cabrales wrote that further research on O. couesi and related species would certainly result in the recognition of additional species .

A 2010 study by Delton Hanson and colleagues used DNA sequence data from the mitochondrial gene cytochrome b (Cytb) and two nuclear markers , exon 1 of the interphotoreceptor retinoid @-@ binding protein gene (Rbp3) and intron 2 of alcohol dehydrogenase gene 1 (Adh1 @-@ I2) to study relationships among populations of the marsh rice rat and O. couesi . The Cytb data placed all studied specimens of O. couesi in a clade sister to the marsh rice rat ; the mean genetic distance between the two groups was 11 @.@ 30 % , much larger than the distance between sister species in the related genera Melanomys and Nectomys (7 @.@ 48 % and 7 @.@ 52 % , respectively) . Within the O. couesi clade , two populations from Panama and Costa Rica were successively basal to the other specimens , which fell into two large subclades ? one containing animals from the Pacific seaboard from western Mexico to El Salvador and the other containing rats from the eastern seaboard from Texas to Nicaragua . The Panamanian and Costa Rican populations differed by 6 @.@ 53 % to 11 @.@ 93 % from the others and the western and eastern subclades differed by 4 @.@ 41 % on average . Data from both of the slower @-@ evolving nuclear markers Rbp3 and Adh1 @-@ I2 also placed examples of Oryzomys in two main clades , but did not recover the western and eastern groups of O. couesi as separate clades . In addition , Adh1 @-@ I2 placed the Costa Rican population within the marsh rice rat clade and placed some western O. couesi specimens closer to the marsh rice rat than to the O. couesi group . The combined dataset supported the western and eastern clades within O. couesi and placed the Costa Rican population marginally closer to the marsh rice rat than to O. couesi . Using the genetic species concept , the authors suggested that the four groups they found within O. couesi should be recognized as distinct species . If this suggestion is followed , the eastern subclade would retain the name Oryzomys couesi , the western group would be named Oryzomys mexicanus , and the appropriate names for the Panamanian and Costa Rican species remain unclear .

= = = Western Mexico to El Salvador = = =

Populations of Oryzomys couesi from Jalisco , western Mexico , east to El Salvador form a single

Cytb clade , which Hanson and colleagues proposed to recognize as the species Oryzomys mexicanus . These animals differ by 4 @.@ 4 % from Oryzomys couesi in the strict sense , which occurs to the north and east , are separated by mountain ranges from the latter , harbor different species of hantavirus , and according to Merriam (1901) have more robust skulls , with larger molars , stronger zygomatic arches (cheekbones) , and better developed ridges along the margins of the interorbital region of the skull (between the eyes) . Within the " Oryzomys mexicanus " clade , Cytb sequence differences average 2 @.@ 06 % and western (Jalisco to Oaxaca) and eastern (Chiapas and El Salvador) groups form distinct subclades ; Hanson and colleagues recognized these as different subspecies , mexicanus in the west and zygomaticus in the east .

As defined by Carleton and Arroyo @-@ Cabrales in 2009 , the subspecies Oryzomys couesi mexicanus occurs along the Pacific coast from central Sonora to southeastern Oaxaca and inland along rivers into central Michoacán , southern Morelos , southern Puebla , and northwestern Oaxaca . It usually lives below 1 @,@ 000 m (3 @,@ 300 ft) altitude , but has been found at 1 @,@ 525 m (5 @,@ 003 ft) in Jalisco . This distributional pattern is similar to that of other western Mexican rodents such as Sigmodon mascotensis , Hodomys alleni , Peromyscus perfulvus , and Osgoodomys banderanus and has been recognized as a distinct biogeographic zone in some reviews . O. c. mexicanus occurs close to three other Oryzomys species ? O. albiventer , O. peninsulae , and O. nelsoni ? which are larger and different in some proportions and details of coloration .

Joel Asaph Allen first described Oryzomys mexicanus as a full species in 1897 from specimens from Jalisco . In the same publication , he also described Oryzomys bulleri from nearby Nayarit , but he did not compare the two with each other . Merriam added a second species from Nayarit , Oryzomys rufus , in 1901 , noting that it was smaller and more reddish than mexicanus . Goldman synonymized the three as O. couesi mexicanus in 1918 and in 2009 Carleton and Arroyo @-@ Cabrales concurred , arguing that the differences between rufus and mexicanus were age @-@ related and within the normal range of variation of the animal . Another subspecies , Oryzomys couesi lambi , was described by Burt in 1934 from central coastal Sonora , which extended the range of the species by 400 mi (640 km) at the time . This form is dark gray @-@ brown , much darker than mexicanus , and has a shorter tail and weaker jugals . Carleton and Arroyo @-@ Cabrales wrote that it is similar to mexicanus , but that further research is needed to determine whether it should be recognized as a subspecies . Large O. couesi from northern Sinaloa may also belong to this form . Goldman wrote that mexicanus was very similar to nominate couesi , but usually with paler fur ; the upperparts are more buffy than in couesi and the underparts are usually white , but may be buffy , the normal color in couesi .

Oryzomys zygomaticus was first described by Merriam in 1901 as a separate species similar to mexicanus , but with the zygomatic arches broadly spreading and curved downward . Goldman , who reduced it to a subspecies of couesi , recorded it from southwestern Guatemala and nearby Chiapas and described it as slightly paler than O. c. couesi but darker than O. c. mexicanus . Three specimens from central El Salvador have Cytb sequences similar to those of zygomaticus , but in The Mammals of El Salvador (1961) , Burt and Stirton recorded only the subspecies couesi from the country , while noting that specimens from some localities were slightly paler than others .

= = = Interior Mexico = = =

Goldman grouped four subspecies of couesi from the interior plateaus of central Mexico together ? albiventer , crinitus , aztecus , and regillus . Three of those (albiventer from Jalisco , crinitus from the Distrito Federal , and aztecus from Morelos) were described by Merriam in 1901 , and Goldman had himself described regillus from Michoacán in 1915 . According to Goldman , aztecus is pale and large @-@ toothed , crinitus is large , dark and large @-@ toothed , regillus is large and dark , and albiventer is large and relatively pale .

In their 2009 review of western Mexican Oryzomys , Carleton and Arroyo @-@ Cabrales classified Oryzomys albiventer as a separate species from lowland mexicanus on the basis of clear morphometric differentiation and offered some comments on the status of crinitus , regillus , and

aztecus , including the holotypes of the three forms in their morphometric analyses . The holotypes of regillus and aztecus were at the upper end of the range of variation in their large series of mexicanus from the western lowlands , and crinitus clustered with specimens of O. peninsulae from the tip of the Baja California Peninsula . They suggested that regillus and aztecus may represent no more than robust upland populations of mexicanus , but could not exclude the possibility that they represent a different species . That crinitus , which occurs at over 2 @,@ 000 m (6 @,@ 600 ft) altitude in the Valley of Mexico , was the same species as peninsulae from the lowlands of the Baja California Peninsula they could not accept and they recommended further research to determine the relationships of crinitus . A specimen from inland Michoacán has Cytb data characteristic of mexicanus , but Hanson and colleagues did not have data for other interior Mexican Oryzomys .

The holotype of the species Oryzomys fulgens , which Thomas had described in 1893 , has no more precise locality than " Mexico " , but the Valley of Mexico has been suggested as its origin . It is a large , coarse @-@ furred , bright reddish , long @-@ tailed species with a broad skull with widely spreading zygomatic arches . Goldman wrote that it was similar to crinitus , but more intensely colored , and differed in the form of the interorbital region ; he retained it as a separate species pending further investigations . Carleton and Arroyo @-@ Cabrales noted that archival research may yet uncover the precise origin of O. fulgens , which could establish it as an older name for one of the other central Mexican Oryzomys .

= = = Texas to Nicaragua = = =

Oryzomys populations from Texas to Nicaragua form a single Cytb clade , within which the average sequence divergence is 1 @.@ 28 % , and Hanson and colleagues proposed that the name Oryzomys couesi be restricted to this clade . These populations correspond to two subspecies recognized by Goldman (O. c. aquaticus and O. c. couesi) and an island form he retained as a species (O. cozumelae) . Two other subspecies Goldman recognized , O. c. richmondi and O. c. peragrus , and a third , O. c. pinicola , that was described after Goldman 's paper occur in the same region , but have not been studied genetically .

The northernmost populations of Oryzomys couesi , those in southernmost Texas and nearby Tamaulipas , Mexico , are classified as the subspecies aquaticus , which was described as a separate species , Oryzomys aquaticus , in 1891 . Here the range of O. couesi meets that of the marsh rice rat ; in parts of Kenedy , Willacy and Cameron counties , Texas , and in far northeastern Tamaulipas , the two are sympatric (occur in the same places) . In the contact zone , couesi occurs further inland , while the marsh rice rat lives along the coast . In experimental conditions , the two fail to interbreed and genetic analysis yields no evidence of gene flow or hybridization in the wild . Compared to populations further to the south , aquaticus is larger and paler and has a more robust skull . Specimens from Tamaulipas are slightly darker than those from Texas . The Cytb sequences of specimens of aquaticus form a separate group , but cluster among specimens of O. c. couesi from further south .

The form peragrus is known from further south in Mexico , in the Río Verde basin of San Luis Potosi , the state of Hidalgo , and far northern Veracruz . Late Pleistocene fossils of this form have been found in Cueva de Abre , Tamaulipas . According to Goldman , it is intermediate in color between O. c. aquaticus and O. c. couesi , but has a skull similar to that of aquaticus .

Goldman united populations ranging from northern Veracruz through eastern Mexico , Guatemala , Honduras , and Nicaragua south to far northwestern Costa Rica in the nominate subspecies , Oryzomys couesi couesi . He placed six other names as full synonyms of this form , which has its type locality in Guatemala ? Oryzomys jalapae Allen and Chapman , 1897 , from Veracruz ; Oryzomys jalapae rufinus Merriam , 1901 , from Veracruz ; Oryzomys teapensis Merriam , 1901 , from Tabasco ; Oryzomys goldmani Merriam , 1901 , from Veracruz ; Oryzomys jalapae apatelius Eliot , 1904 , from Veracruz ; and Oryzomys richardsoni Allen , 1910 , from Nicaragua . According to Goldman , individual variation within the subspecies is large , which has led to the large number of published synonyms , but populations from all parts of its range are essentially similar .

The subspecies Oryzomys couesi pinicola was described in 1932 from a pine ridge in western

British Honduras (now Belize) ; it is smaller and darker than nominate couesi , which also occurs in Belize , and has a more delicate skull . In 1901 , Merriam described the Oryzomys of the island of Cozumel as a separate species , Oryzomys cozumelae , and Goldman kept it as such because of its large size , dark fur , and long tail . In 1965 , however , Knox Jones and Timothy Lawlor judged the differences between cozumelae and mainland couesi trivial and found that cozumelae was inside the range of variation of mainland Oryzomys populations ; accordingly , they demoted the island form to a subspecies . Mark Engstrom and colleagues , writing in 1989 , reaffirmed this conclusion . For an island form , this population is highly genetically variable . In its Cytb sequence data , it falls among populations of nominate couesi . Oryzomys couesi is also found on Turneffe Atoll off the coast of Belize and Roatán off Honduras .

The Oryzomys of the eastern lowlands of Nicaragua was described as a separate species , Oryzomys richmondi , by Merriam in 1901 , and Goldman retained it as a subspecies of O. couesi on the basis of its distinctly dark fur . In reviewing Nicaraguan Oryzomys in 1986 , Jones and Engstrom did not keep richmondi as separate , because they thought the difference in color too small for the recognition of subspecies . Oryzomys dimidiatus , a small , dark Oryzomys with gray underparts , occurs with O. couesi in southeastern Nicaragua . According to Jones and Engstrom , rice rats from the island of Ometepe in Lake Nicaragua are distinctive in their large skull and small external measurements , with an especially short tail , soft fur that is orange @-@ brown above and buffish below , and lack of sphenopalatine vacuities (openings in the roof of the mesopterygoid fossa , the gap behind the end of the bony palate) . They considered that this population probably represented a separate subspecies , but declined to propose a new name because they had only one adult specimen . In Nicaragua , O. couesi occurs up to an altitude of 1 @,@ 250 m (4 @,@ 100 ft) .

= = = Costa Rica , Panama , and Colombia = = =

Oryzomys from Costa Rica have historically been referred to O. c. couesi , but Hanson and colleagues found that two specimens from Refugio Nacional de Vida Silvestre Mixto Maquenque , northeastern Costa Rica , differed as much from other O. couesi (11 @.@ 93 % Cytb sequence divergence) as O. couesi differed from the marsh rice rat (11 @.@ 30 %) . They suggested that these animals represented a species distinct from O. couesi , but were unable to resolve the correct name for the species because they could not examine samples of dimidiatus or richmondi .

Oryzomys is rare in Panama . Panamanian Oryzomys were first described by Goldman in 1912 , who introduced the name Oryzomys gatunensis for a specimen from Gatún in the Canal Zone . In 1918 , Goldman kept the animal as a separate species , remarking that it was similar to richmondi , but distinctive in the well @-@ developed ridges along the margins of the interorbital region , the short interparietal bone (part of the roof of the braincase) , and the long nasal bones . In 1937 , Bole described another species of Panamanian Oryzomys , Oryzomys azuerensis from Paracoté , Veraguas Province . It is a brown form , lacking the reddish tones of nearby populations , and has a broad skull with a short rostrum (front part) and ridges on the interorbital region like those of gatunensis . Although Goldman recommended to him that gatunensis and azuerensis both be treated as subspecies of couesi , Bole described azuerensis as a species because it did not seem intermediate between the geographically closest forms , gatunensis and couesi , and was separated by a large gap from the nearest known populations of O. couesi in northwestern Costa Rica and southeastern Nicaragua . In a 1966 review of Panamanian mammals , Charles Handley reduced both gatunensis and azuerensis to subspecies of the marsh rice rat (in which O. couesi was included at the time) , and when O. couesi was reinstated as a separate species these forms went with it . Specimens from near the type locality of azuerensis differ by about 7 % in their Cytb sequences from other O. couesi , which suggests that they may represent a separate species . However , Hanson and colleagues did not reinstate azuerensis as a species , because they could not examine samples of gatunensis .

Oryzomys couesi was first reported from Colombia in 1987 , when Philip Hershkovitz reported on its occurrence at Montería in Córdoba Department , northwestern Colombia . The Colombian specimen

is ochraceous in color throughout and according to Hershkovitz almost identical to specimens from Guatemala , but distinctive in that the upper lip is white . He suggested that O. couesi may also be discovered in the Pacific lowlands of the Chocó in western Colombia .

= = = Common names = = =

Several common names have been proposed for Oryzomys couesi and the synonyms currently associated with it . Eliot in 1905 and Goldman in 1918 gave separate common names for each of the species and subspecies they recognized . Many authors have used " Coues ' Rice Rat " or some variation thereof for O. couesi , but " Coues ' Oryzomys " has also been used .

= = Description = =

Oryzomys couesi is a medium @-@ sized to large rat with coarse fur that is buff to reddish above , becoming paler towards the sides and cheeks and darker on the rump and face . The underparts are white to buff . The fur is shorter , brighter , and more intense in color than in the marsh rice rat . The snout ends bluntly and the moderately large eyes show reddish eyeshine . The small ears are black on the outside and the inside is covered with short , gray to buff or red hairs . The long tail is dark brown above and white to light brown below . The feet are long and stout . On the forefeet , the ungual tufts (tufts of hair on the digits) are present . Many of the pads on the hindfeet are reduced , as are the ungual tufts , and small interdigital webs may be present in at least some specimens . Some of these traits are common adaptations to life in the water in oryzomyines . As in most other oryzomyines , females have eight mammae . Head and body length is 98 to 142 mm (3 @.@ 9 to 5 @.@ 6 in) , tail length is 107 to 152 mm (4 @.@ 2 to 6 @.@ 0 in) , hindfoot length is 27 to 33 mm (1 @.@ 1 to 1 @.@ 3 in) , ear length is 13 to 18 mm (0 @.@ 51 to 0 @.@ 71 in) , and body mass is 43 to 82 g (1 @.@ 5 to 2 @.@ 9 oz) . Studies in Texas and El Salvador found that males are slightly larger than females .