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60) . The form of the sex chromosomes has been used to distinguish the marsh rice rat from *Oryzomys couesi* , but may be too variable among *Oryzomys* to be useful in differentiating species . X chromosome inactivation occurs in the marsh rice rat , even though the animal lacks LINE @-@ 1 retrotransposons , which have been suggested as components of the inactivation process . Mutants with fused or additional molars and with light fur have been recorded in laboratory colonies ; the abnormal molars are apparently the result of a single autosomal recessive mutation . At about 50 % , hematocrit (the proportion of red blood cells in the blood) is high in the marsh rice rat compared to other rodents ; this may be an adaptation that enables the rice rat to increase oxygen capacity while swimming underwater .

= = = Male reproductive anatomy = = =

The glans penis is long and robust , averaging 7 @. @ 3 mm (0 @. @ 29 in) long and 4 @. @ 6 mm (0 @. @ 18 in) broad , and the baculum (penis bone) is 6 @. @ 6 mm (0 @. @ 26 in) long . As is characteristic of Sigmodontinae , the marsh rice rat has a complex penis , with the distal (far) end of the baculum ending in three digits . The central digit is notably larger than those at the sides . The outer surface of the penis is mostly covered by small spines , but there is a broad band of nonspinous tissue . The papilla (nipple @-@ like projection) on the dorsal (upper) side of the penis is covered with small spines , a character the marsh rice rat shares only with *Oligoryzomys* and *Oryzomys couesi* among oryzomyines examined . On the urethral process , located in the crater at the end of the penis , a fleshy process (the subapical lobule) is present ; it is absent in all other oryzomyines with studied penes except *O. couesi* and *Holochilus brasiliensis* . The baculum is deeper than it is wide .

Some features of the accessory glands in the male genital region vary among oryzomyines . In the marsh rice rat , a single pair of preputial glands is present at the penis . As is usual for sigmodontines , there are two pairs of ventral prostate glands and a single pair of anterior and dorsal prostate glands . Part of the end of the vesicular gland is irregularly folded , not smooth as in most oryzomyines .

= = = Skull = = =

The marsh rice rat has a large , flattened skull with a short and broad rostrum (front part) . The nasal and premaxillary bones extend back beyond the point where the lacrimal , frontal , and maxillary bones meet . In planirostris , the rostrum is flatter than in mainland Florida forms , in which it is more convex , and the nasals are said to be relatively longer in *argentatus* . The zygomatic plate , the flattened front part of the zygomatic arch (cheekbone) , is broad and develops a notch at its front end . The arches themselves are robust and contain small but distinct jugal bones . The sphenopalatine foramen , a foramen (opening) in the side of the skull above the molars , is large ; it is much smaller in *O. couesi* . The narrowest part of the interorbital region (located between the eyes) is towards the front and the edges are lined by prominent shelves . The marsh rice rat has a narrow braincase lined by prominent ridges and a narrow interparietal bone . According to Goldman , Florida animals (*coloratus* and *natator*) generally have the largest and broadest skulls , and western specimens (*texensis*) have somewhat smaller and narrower skulls than those from the east outside Florida (*nominate palustris*) . In *argentatus* , the skull is also relatively narrow .

The incisive foramina , openings in the front part of the palate , reach backward between the molars . The palate is long , extending substantially beyond the third molars . The back part , near the third molars , is usually perforated by prominent posterolateral palatal pits , which are recessed into fossae (depressions) . The mesopterygoid fossa , the gap behind the end of the palate , is perforated by sphenopalatine vacuities , which are set far to the front . The condition of the arteries in the head is highly derived . The subsquamosal fenestra , an opening in the back part of the skull determined by the shape of the squamosal bone , is present . The squamosal lacks a suspensory process that contacts the tegmen tympani , the roof of the tympanic cavity , a defining character of

oryzomyines . There are some openings in the mastoid bone .

In the mandible (lower jaw) , the mental foramen , an opening just before the first molar , opens sideways , not upwards as in a few other oryzomyines . The upper and lower masseteric ridges , which anchor some of the chewing muscles , join at a point below the first molar and do not extend forward beyond that point . The capsular process , a raising of the bone of the back of the mandible that houses the back end of the incisor , is present , but not as large as in *O. couesi* .

== Teeth ==

The dental formula is $1 \frac{.}{.} 0 \frac{.}{.} 0 \frac{.}{.} 31 \frac{.}{.} 0 \frac{.}{.} 0 \frac{.}{.} 3 \times 2 = 16$ (one upper and one lower incisor and three upper and three lower molars) , as usual in muroid rodents . The upper incisors are well developed and strongly opisthodont , with the chewing edge located behind the vertical plane of the teeth . The molars are bunodont , with the cusps higher than the connecting crests , and brachydont , low crowned , as in most other oryzomyines . Many accessory crests , including the mesoloph on the upper molars and the mesolophid on the lower molars , are present , another trait the marsh rice rat shares with most but not all other oryzomyines . The flexi and flexids (valleys between the cusps and crests) at the labial (outer) side of the molars are closed by cingula (ridges) .

The upper molars have two longitudinal rows of cusps , not three as in the black and brown rats . The first and second upper molar are oval in form and the flexi do not extend to the midline of the molars . The anterocone , the front cusp of the upper first molar , is not divided in two by an indentation at its front (anteromedian flexus) , but does display a hollow in the middle , the anteromedian fossette , which divides it into separate cuspules at the labial and lingual (inner) sides of the molar . A crest , the anteroloph , is present behind the labial cuspule , but in older animals , the cusps and the crest are united into a single structure by wear . In the third upper molar , the cusps at the back are reduced and scarcely distinguishable . As in most oryzomyines , the upper molars all have one root on the inner (lingual) side and two on the outer (labial) side ; in addition , the first upper molar usually has another small labial root .

The first lower molar is rounded at the front end and the labial and lingual conules of the anteroconid , the frontmost cusp , are barely distinct . The second lower molar is elongate and has a crest , the anterolophid , before the two cusps that form the front edge of the molar in some other oryzomyines , the protoconid and metaconid . There is a distinct ridge (anterolabial cingulum) at the outer front (anterolabial) edge of the molar , before the protoconid . The lower third molar is about as long as the second and also has an anterolophid , albeit a less well defined one . The first lower molar has large roots at the front and back of the tooth and usually one or two smaller ones in between , at the labial and lingual side . The second and third lowers molars have either two roots , one labial and one lingual , or only one at the front , and another large root at the back .

== Postcranial skeleton ==

As usual in oryzomyines , there are twelve ribs . The first rib articulates with both the last cervical (neck) and first thoracic (chest) vertebrae , a synapomorphy of the Sigmodontinae . Anapophyses , processes at the back of a vertebra , are absent from the fifth lumbar . Between the second and third caudal vertebrae , hemal arches (small bones) are present with a spinous back border . The entepicondylar foramen is absent , as in all members of the Sigmodontinae ; if present , as in some other rodents , this foramen perforates the distal (far) end of the humerus (upper arm bone) .

== Physiology ==

Studies have shown that in poor conditions the weight of the adrenal gland may increase up to 200 % , that rice rats are unable to conserve water well when dehydrated , and that in water contaminated with oil they swim less and their mortality increases . The median amount of radiation needed to kill a marsh rice rat is $5 \frac{.}{.} 25$ Gy and the lethal dose of potassium cyanide is $7 \frac{.}{.}$

20 mg / kg ; both values are relatively low for cricetid rodents . In one study , wild rice rats in radioactively contaminated areas did not show signs of disease . Experiments have found that exposure to more daylight and higher food availability cause increased development of the gonads in both adult and juvenile rice rats . When the pineal gland is removed or melatonin is administered in male rice rats , the testes are reduced and tend to regress into the body .

= = Distribution and habitat = =

The marsh rice rat currently occurs in much of the eastern and southern United States , northeast to southern New Jersey , and south to southeastern Texas and far northeastern Tamaulipas , Mexico . The northernmost records in the interior United States are in eastern Oklahoma , southeastern Kansas , southern Missouri and Illinois , and the southern half of Kentucky , but the species is absent in much of the Appalachians . Fossils of the marsh rice rat are known from Rancholabrean (late Pleistocene , less than 300 @, @ 000 years ago) deposits in Florida and Georgia and remains referred to the extinct subspecies *O. p. fossilis* are from the Wisconsinan and Sangamonian of Texas and Illinoian and Sangamonian of Kansas . In the Florida Keys , rice rats occur on most of the Lower Keys , but are absent from the Upper Keys , which are of a different geological origin and were probably never connected to the mainland . The western and eastern Cytb clades within the marsh rice rat may represent expansions from different glacial refugia which the species was restricted to during a glacial period .

Cave and archeological remains indicate that the range of the marsh rice rat has extended substantially further north and west earlier in the Holocene , into central Texas , eastern Nebraska , southwestern Iowa , central Illinois , southern Indiana , southern Ohio , West Virginia , and southwestern Pennsylvania . Most northern archeological sites date from about 1000 CE and are associated with corn cultivation , but in some older cave sites the rice rat is found with the extinct giant armadillo *Dasypus bellus* , suggesting warm climatic conditions . Perhaps a warm period during the Quaternary enabled the rice rat to disperse northward and when the climate cooled , relict populations were able to survive in the north as commensals in corn @-@ cultivating Native American communities . Some subfossil animals are slightly larger than living marsh rice rats , possibly because environmental constraints were relaxed in commensal populations .

In Tamaulipas and southern Texas , the ranges of the marsh rice rat and the related *Oryzomys couesi* meet ; in parts of Kenedy , Willacy and Cameron counties , Texas , and in far northeastern Tamaulipas , the two are sympatric (occur in the same places) . In experimental conditions , they fail to interbreed and genetic analysis yields no evidence of gene flow or hybridization in the wild . Compared to *O. couesi* , the marsh rice rat shows less genetic variability within but more between populations in the contact zone , probably because the species is restricted to isolated populations near the coast .

The marsh rice rat occurs in several habitats , ranging from coastal salt marshes to mountain streams and clearings . It is semiaquatic , spending much time in the water , and usually occurs in wetland habitats . It prefers areas where the ground is covered with grasses and sedges , which protect it from predators . In southern Illinois , marsh rice rats are more likely to occur in wetlands with more herbaceous cover , visual obstruction , and nearby grasslands . The species also occurs in drier uplands , which serve as sinks for young , dispersing animals and as refuges during high tide . Rice rats are adept overwater dispersers ; studies on islands off Virginia 's Delmarva Peninsula show that they readily cross 300 @-@ m (1000 ft) channels between islands .

= = Behavior and ecology = =

Marsh rice rats are active during the night and for this reason are rarely seen , although they may be among the most common small mammals in part of their range . They will build nests of sedge and grass , about 13 cm (5 in) large , which are placed under debris , near shrubs , in short burrows , or high in aquatic vegetation . They may also use old nests of marsh wrens (*Cistothorus palustris*) , red @-@ winged blackbirds (*Agelaius phoeniceus*) , muskrats (*Ondatra zibethicus*) or

round @-@ tailed muskrats (*Neofiber alleni*) . Marsh rice rats sometimes make large runways or dig burrows . They are accomplished and willing swimmers , easily swimming for more than 10 m (33 ft) under water , and will often seek safety in the water when alarmed . Rice rats in the Florida Keys occasionally climb in vegetation , but never higher than 90 cm (3 @.@ 0 ft) . Marsh rice rats are very clean and extensively groom themselves , perhaps to keep their fur water @-@ repellent . They are aggressive towards conspecifics and emit high @-@ pitched squeaks while fighting . In dense vegetation , the perceptual range (the distance from which an animal can detect a patch of suitable habitat) of marsh rice rats is less than 10 m (33 ft) . When released outside of their natural wetland habitat , marsh rice rats generally move either upwind or downwind (anemotaxis) , perhaps in order to move in a straight line , which is an efficient strategy to find suitable habitat .

Many animals prey on marsh rice rats . The barn owl (*Tyto alba*) is among the most important ; one study found that 97 @.@ 5 % of vertebrate remains in barn owl pellets were marsh rice rats . Other predators include birds (marsh hawks , *Circus cyaneus* ; and barred owls , *Strix varia*) , snakes (cottonmouth moccasins , *Agkistrodon piscivorus* ; and others) , alligators , and carnivorans (raccoons , *Procyon lotor* ; red foxes , *Vulpes vulpes* ; minks , *Neovison vison* ; weasels of the genus *Mustela* ; and striped skunks , *Mephitis mephitis*) . Many parasites have been recorded on the marsh rice rat , including various ticks and mites , lice , and fleas among external parasites and many nematodes and digeneans , a pentastomid , and several coccidians among internal parasites (see parasites of the marsh rice rat) .

Periodontitis , a bacterial disease affecting the jaws , is particularly virulent in marsh rice rats ; the animal has been proposed as a model for research on the disease in humans . The identity of the bacterial agent remains unknown . Vitamin E , fluoride , and iodide protect against bone loss associated with this disease in the rice rat and a high @-@ sucrose diet increases the severity of periodontitis . A case of kyphosis has been observed in a North Carolina marsh rice rat .

= = = Population dynamics = = =

The population density of the marsh rice rat usually does not reach 10 per ha (4 per acre) . The weather may influence population dynamics ; in the Everglades , densities may exceed 200 per ha (80 per acre) when flooding concentrates populations on small islands , In the Florida Keys , population density is less than 1 per ha (0 @.@ 4 per acre) . On Breton Island , Louisiana , perhaps an atypical habitat , home ranges in males average about 0 @.@ 37 hectares (0 @.@ 91 acres) and in females about 0 @.@ 23 hectares (0 @.@ 57 acres) . A study in Florida found male home ranges to average 0 @.@ 25 hectares (0 @.@ 62 acres) and female 0 @.@ 33 hectares (0 @.@ 82 acres) .

Population size is usually largest during the summer and declines during winter , although populations in Texas and Louisiana may be more seasonally stable . Animals also often lose weight during winter . Population size varies dramatically from year to year in southern Texas . In coastal Mississippi , a study found that storms probably do not cause the population to decline substantially and in Texas inundation of its habitat did not significantly influence population density . However , another study in Mississippi found that flooding did cause a marked decline in rice rat abundance .

In the northern part of its range , the species often occurs with the meadow vole (*Microtus pennsylvanicus*) , but there is no evidence that they compete with each other . In the south , the hispid cotton rat (*Sigmodon hispidus*) and the rice rat regularly occur together ; water levels are known to influence relative abundance of these two species in Florida . The cotton rat is mainly active during the day , which may help differentiate its niche from that of the rice rat .

= = = Diet = = =

The marsh rice rat takes both vegetable and animal food , and is more carnivorous than most small rodents are ; dominant food items vary seasonally . Plants eaten include species of *Spartina* , *Salicornia* , *Tripsacum* , and *Elymus* , among others ; it mainly eats seeds and succulent parts . A 2004 study found that it prefers *Spartina alterniflora* that have been fertilized with nitrogen and

mainly eats the inner tissue of the stem , perhaps because nitrogen @-@ fertilized plants contain much less dimethylsulfoniopropionate in their inner tissues . The marsh rice rat was a major pest on rice plantations , feeding on the rice when it was newly planted . It also eats the fungus *Endogone* at times .

Animals that are important to the marsh rice rat 's diet include insects , fiddler crabs , and snails , but the species is known to eat many other animals , including fish , clams , and juvenile *Graptemys* and *Chrysemys* turtles . They scavenge on carcasses of muskrats , deermice , and sparrows , and may be the most important predator on eggs and young of the marsh wren . Rice rats also eat eggs and young of the seaside sparrow (*Ammodramus maritimus*) and are aggressive towards the sparrow , apparently leading it to avoid nesting in *Juncus* in a seaside salt marsh in Florida . On islands in North Carolina , rice rats consume eggs of Forster 's tern (*Sterna forsteri*) . They have been observed preying on alligator eggs in Georgia .

Laboratory studies have found that rice rats assimilate 88 % to 95 % of the energy in their food . They lose weight when fed on *Spartina* , fiddler crabs , or sunflower seeds alone , but a diet consisting of several of those items or of mealworms is adequate to maintain weight . In an experiment , marsh rice rats did not show hoarding behavior , but wild rice rats have been observed carrying food to a nest . Even when they live in uplands , they mostly eat water plants and animals , although they consume some upland plants .

= = = Reproduction and life cycle = = =

Breeding occurs mostly during the summer . Some studies report that breeding ceases entirely during the winter , but winter breeding occurs as far north as Virginia . This is primarily because photoperiod influences their circadian rhythm which determines breeding . In both Texas and Virginia , there is less variation in reproductive activity in females than in males . In the south of its range , animals may breed less when the summer is at its warmest . The duration of the estrous cycle ranges from 6 to 9 days , with an average of 7 @.@ 72 days . Estrus occurs again after a litter is born . A 1970 study reported that copulatory behavior in the marsh rice rat is similar to that in laboratory brown rats . Before mating starts , " the male pursues the running female from behind . " The male then repeatedly mounts and dismounts the female ; not all mounts result in an ejaculation . Penetrations only last for about 250 ms , but during mating the penetrations and the intervals between them become longer . Even when a male is satiated after mating , it is able to copulate again when a new female is introduced (the Coolidge effect) . Partly because of resistance by the female , the frequency of ejaculation during mating is rather low in marsh rice rats as compared to laboratory rats , hamsters , and deermice .

After a gestation of about 25 days , three to five young are usually born , although litter sizes vary from one to seven . Females may have up to six litters a year . Newborns weigh 3 to 4 g (about 0 @.@ 1 to 0 @.@ 15 oz) and are blind and almost naked . About as many males as females are born . The external ears (pinnae) soon unfold and on the first day claws are visible and the young emit high @-@ pitched squeaks . On the second day , they are able to crawl and during the third to fifth days the whiskers and eyelids develop . On the two subsequent days , the mammae and incisors become visible and the animals become more active . Between the eighth and eleventh day , the eyes open , the fur develops , and the young begin to take solid food . Weaning occurs on the eleventh to twentieth day according to different studies . There is considerable variation in reported body masses at different ages , perhaps because of geographic variation . Sexual activity commences when the animals are about 50 to 60 days old . In the wild , rice rats usually live for less than a year ; one study suggested that the average lifespan is only seven months .

= = Human interactions = =

The marsh rice rat is generally of little importance to humans , which is perhaps why it is not as well @-@ studied as some other North American rodents . In 1931 , Arthur Svihla noted that virtually no information had been published on the habits and life history of the marsh rice rat since the 1854

publication of Audubon and Bachman 's description . Writing on Everglades mammals , Thomas E. Lodge notes that although the name " rat " may associate it unpleasantly with the introduced black and brown rats , its appearance is more endearing , even cute . J.S. Steward proposed the marsh rice rat as a model organism in 1951 to study certain infections that other rodents used at the time are not susceptible to . The marsh rice rat is quite susceptible to periodontitis and has been used as a model system for the study of that disease .

The marsh rice rat is the primary host of the Bayou virus (BAYV) , the second most common agent of hantavirus infections in the United States . About 16 % of animals are infected and the virus is most prevalent in old , heavy males . The virus may be transmitted among rice rats through bites inflicted during fights . It is also present in rice rat saliva and urine and human infections may occur because of contact with these excreta . Two related hantaviruses , Catacama virus and Playa de Oro virus , are known from *Oryzomys couesi* in Honduras and western Mexico , respectively . An arenavirus normally associated with woodrats (*Neotoma*) has also been found in Florida marsh rice rats . Antibodies against *Borrelia burgdorferi* , the bacterium that causes Lyme disease in the United States , have been found in marsh rice rats in Virginia , Maryland , North Carolina , and Tennessee . Another pathogenic bacterium , *Bartonella* , is known from Georgia marsh rice rats .

The 2009 IUCN Red List assesses the conservation status of the marsh rice rat as " Least Concern " , because it is a common , widespread , and stable species without major threats that occurs in several protected areas . The Florida Keys form is rare and in decline and is threatened by competition with the black rat , predation by domestic cats , habitat loss , and loss of genetic variation ; it is considered endangered . At the northern edge of its distribution , the marsh rice rat is listed as threatened in Illinois and whether it persists in Pennsylvania is unclear ; it probably formerly occurred in tidal marshes on the Delaware River . In Illinois , its population may have regenerated because wetlands have been developed to protect waterfowl and shorebirds and because suitable wetlands often develop in abandoned coal @-@ mining operations . A 2001 study projected that climate change would reduce the range of the marsh rice rat in Texas , where it is now common but may become threatened by habitat loss in the future . A study at the Paducah Gaseous Diffusion Plant found that rice rats accumulate more PCBs but less heavy metal than white @-@ footed mice (*Peromyscus leucopus*) .