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Callithrix pygmaea. By Wendy R. Townsend

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Callithrix pygmaea (Spix, 1823) Pygmy Marmoset

Iacchus pygmaeus Spix, 1823:32. Type locality "Tabatinga, Rio Solimoes, Amazonas, Brasil."

Cebuella pygmaea Gray, 1870:64. Renaming of Iacchus pygmaeus Spix.

Callithrix pygmaea Elliot, 1913:232. First use of current name combination.

Callithrix pygmaea niveiventris Lönnberg, 1940:21. Type locality "Lago do Ipoxona, Amazonas, Brasil."

CONTEXT AND CONTENT. Order Primates, family Callithricidae. The genus *Callithrix* contains 10 species. No subspecies of *C. pygmaea* are recognized (Mittermeier et al. 1988; Wilson and Reeder 1993).

DIAGNOSIS. The smallest New World primate, *Callithrix* pygmaea, can be distinguished from other Callithricidae not only by its small size but also by the heavy mane, barred tail, squirrellike hands and feet, and general dark golden and speckled color of upper body parts (Fig. 1). Confusion with immature *Callithrix jacchus* can be avoided by noting the latter's lack of speckled or grizzled coloring on head, cheeks, and mantle. All other neotropical primates are 3–5 times larger in size or distinct in coloration (Eisenberg 1989).

GENERAL CHARACTERS. Dorsal pelage of *C. pygmaea* is tawny and darker speckled pattern may extend over rump and form a semistriated pattern in adults (Soini 1988). Long hair forms a mane surrounding face and nape, almost completely concealing ears. Ventral pelage varies among individuals from tawny to buffy, but completely white venters occur only in adults (Soini 1988). Face is well-furred and exhibits a buffy patch across nasal ridges and often a conspicuous mustache. Tail is partially to completely ringed with darker rings on a lighter background. Genital area can be pigmented or not and is framed by black pelage (Soini 1988). Pelage color of *Callithrix pygmaea* does not vary with sex or age. In captivity, 2 phenotypes are recognized: yellow-belly and whitebelly. Yellow-belly males have pigmented spots on the scrotum, which white-belly males lack (Albers 1990).

Females are 12% heavier than males (Soini 1988). Length of head and body (in mm) of 42 adults averaged 137 (range, 120– 152—Herskovitz 1977). Average total length of 63 adults was 339 mm (331–362); mean body mass of the same individuals was 119 g (85–140—Soini 1988). The nonprehensile tail ranges from 172– 229 mm in length (Emmons 1997), which is ca. 60% of total length (Hershkovitz 1977; Soini 1988).

Frontal contour of skull (Fig. 2) is convex and nasal profile is slightly concave. Temporal ridges are only weakly defined, but auditory bullae are well inflated. Outline of inferior border of mandible is v-shaped (Hershkovitz 1977). Measurements (in mm, range and sample size in parentheses) are: greatest length, 35.8 (33.7– 38.9, 61); length of braincase, 30.9 (28.3–32.8, 62); and width of braincase, 21.1 (20.0–22.9, 61—Hershkovitz 1977). Volume of braincase for 19 individuals was 34.8 cm³ (Hershkovitz 1977).

DISTRIBUTION. Pygmy marmosets inhabit multistrata tropical evergreen forests of the western Amazon basin (Fig. 3). They are distributed south of the Caquetá (Japura) River of Colombia, westward into Amazonian Ecuador, and southward through eastern lowlands of Peru to the right bank of the Ucayali River. They also occur south to the Manu and Madre de Dios Rivers and probably through northern Bolivia. Limits of the southeastern portion of range are poorly documented, but *C. pygmaeae* probably extends to Brazil along the north bank of the Purus River north to

Solimões River (Freese et al. 1982; Hershkovitz 1977; Janson and Emmons 1990; Soini 1988).

FORM AND FUNCTION. Anatomy of Callithrix pygmaea, including comparative drawings and photographs of the integument, external genitalia, cranium, and dental system was described (Hershkovitz 1977). Dental formula is i 2/2, c 1/1, p 3/3, m 2/2, total 32 (Hershkovitz 1977). Upper and lower incisors point slightly forward and inward toward center. Lower canines are about same height as lower incisors, and upper canines are conspicuously taller than adjacent incisors (Hershkovitz 1977). Forward projection of front teeth, a condition described as procumbent (Hernandez-Camacho and Cooper 1976; Moynihan 1976a) or semiprocumbent (Kinzey et al. 1975) is exaggerated by high-crowned incisors. The distinctive and high palatal vault of C. pygmaea may be adaptive for exudate feeding (Coimbra-Filho and Mittermeier 1977) by improving suction (Hershkovitz 1977). Premolars are caniniform, molarization progresses posteriorly, and M2 and m2 are reduced (Hershkovitz 1977; Kanazawa and Rosenberger 1988). Dental enamel of all Callithrix teeth, including C. pygmaea, exhibits a nonserial structural pattern similar to that of Callithrix jacchus (Nogami and Natori 1986).

A brainstem atlas of *C. pygmaea* includes a series of drawings and photographs (Jacobowitz and MacLean 1978). Patterns of organization of 3 recognized aminergic systems of the brain are somewhat similar to rodents (Jacobowitz and MacLean 1978). Postcranial

FIG. 1. Adult female pygmy marmoset *Callithrix pygmaea* carrying young on back. Photograph courtesy of C. H. Snowden.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandibles of *C. pygmaea* from Peru, Loreto, Iquitos, Río Maniti, Santa Cecilia (Field Museum of Natural History, 87135). Greatest length of cranium is 34.6 mm. Photographs courtesy of P. Hershkovitz, previously published in Hershkovitz (1977).

skeletal system has 7 C, 13 T, 6–7 L, 3 S, 28–29 Ca, total 57–59 vertebrae (Hershkovitz 1977).

Pygmy marmosets have more highly specialized and numerous sensory vibrissae than other monkeys (Hershkovitz 1977). These include ulnar, carpal, antebrachial, anconeal, mystacial, mental, interramal, gular, and pectoral vibrissae patches (Hershkovitz 1977).

Pygmy marmosets prefer galactose and to a lesser extent, arabinose, whereas other species of marmosets avoid these sugars (Glaser 1968, 1970). A preference for particular substances might be ecologically significant to interspecific resource partitioning (Glaser and Hobi 1985).

The adult penis is unpigmented, smooth, spineless, and has a baculum that measures 2.7 mm in length and 0.7 mm in width (Hershkovitz 1977; Starck 1969). Scrotum is globose with testes wider than long and prepuce is unpigmented or mottled (Hershkovitz 1977). Female labia majora are glandular, hairy, and some-



FIG. 3. Distribution of *Callithrix pygmaea* in South America (modified from Hershkovitz 1977).

times more or less pigmented (Hershkovitz 1977). Glans clitoridis is concealed in labial tissue, and external genitalia are longer than wide. Perineal and anal regions may be pigmented (Hershkovitz 1977).

ONTOGENY AND REPRODUCTION. Although the pygmy marmoset is a nonseasonal breeder in captivity (Ziegler et al. 1990), 85% of study groups in the wild reproduced during birthing peaks ca. 6 months apart (Soini 1988). Gestation is 19–20 weeks in captivity (Christen 1974) and interbirth intervals range from 145 to 746 days (Ziegler et al. 1990). Minimum age at first parturition in captivity is 32 months (range, 24–42, n = 10—Ziegler et al. 1990). Time between 1st pairing and 1st birth averages 10.5 months (range, 5–27, n = 10—Ziegler et al. 1990). Postpartum estrous occurs 9–18 days after parturition (Soini 1987).

Females most commonly give birth to twins (67–76% of wild and captive births), but single young are not unusual; triplets are rare (Christen 1974; Soini 1988; Ziegler et al. 1990). Neonate is furred except for belly, and eyes are open at birth (Christen 1974).

Developing young have been categorized in the following age classes (Soini 1988): infant 1 (birth to 1 month), very small size, having only deciduous teeth and being carried constantly; infant 2 (2–5 months), also small but locomotion is independent, and 1st molar is present; juvenile (6–12 months), smaller than adult, genitals still small, black circum-anogenital pelage just beginning to appear, face nearly adult-like; and subadult (12–16 months), slightly smaller and leaner than adults, scrotal pigmentation incipient, genitals still smaller than in adults, and canines not yet full size. At ca. 16 months, *C. pygmaea* becomes sexually mature (Soini 1982, 1988; Soini and de Soini 1990a).

Callithrix pygmaea begins erupting its permanent teeth at the end of the 3rd or the beginning of the 4th month (Soini and de Soini 1990b). Milk teeth are shed after 6 months, and by end of the 9th month, all permanent teeth have erupted. Canines reach full length at 15–17 months (Soini and de Soini 1990b). Dental eruption and development sequence is similar to other callithricids (mandible = m1-i1-m2-i2-p3-p2-p1-c1; maxilar = M1-I1-M2-(P3– P2)-(P1–I2)-C1), except that the second incisor erupts after the second molar (Byrd 1978, 1981; Soini and de Soini 1990b). This delayed eruption and development of the incisor is unique among extant primates and may be correlated with the caniniform crown morphology. A developmental-eruptive overlap of the canine field may make simultaneous eruption of both canine and incisor difficult (Byrd 1978).

ECOLOGY. Callithrix pygmaea inhabits lowland tropical evergreen forests of the western Amazon, mostly on flood plains of periodically inundated rivers and streams (Soini 1988). Distribution and density is directly related to presence and abundance of trees used as their food source, such as Quararibea rhombifolia, Vochysia lomatophylla, Trichilia, and Spondias mombin (Ramirez et al. 1977; Soini 1988). Densities vary from 51–59 trees/km² in flood plain forest to 210–233 trees/km² along river edges in Peru (Soini 1988). Their food occurs on black water systems (Ramirez et al. 1977) as well as white water systems that have mixed with local black water streams (Soini 1982). The pygmy marmoset colonizes forest edges and may inhabit edges of old pastures, crop fields, and orchards (Hernandez-Camacho and Cooper 1976; Soini 1988). Microhabitats of *C. pygmaea* consist of heterogeneous edge vegetation and adjoining, mixed forest exhibiting discernible strata, including vines or other dense shelter (Soini 1982).

Pygmy marmosets feed principally on arthropods and exudates vines or trees (Hernandez-Camacho and Cooper 1976; Izawa 1975; Kinzey et al. 1975; Moynihan 1976a, 1976b; Ramirez et al. 1977; Soini 1982). Fruits of Ficus and Pourouma, as well as buds, flowers, and nectar (Ramirez et al. 1977; Soini 1988) are eaten but they are only minor contributors to the diet of pygmy marmosets. Exudates may be either saps or gums (Coimbra-Filho and Mittermeier 1977; Hershkovitz 1977; Ramirez et al. 1977) of over 60 species of trees and vines (Soini 1988). The most common species tapped by this marmoset are Quararibea rhombifolia (Bombacaceaea), Vochysia lomatophylla (Vochysiaceae), Trichilia (Meliaceae), Cheiloclinium cognatum (Hippocrataceae), Spondias mombin (Anacardiaceae), and Parkia oppositifolia (Leguminosae-Hernandez-Camacho and Cooper 1976; Ramirez et al. 1977; Soini 1982, 1988). S. mombin and P. oppositifolia accounted for 66%, V. lomatophylla 44%, and vines 25% of all exudate feeding time (Soini 1988). Sap feeding is facilitated by the pygmy marmoset's dental characteristics, as this primate anchors upper incisors and canines in a fixed position and then scrapes with lower teeth (Coimbra-Filho and Mittermeier 1977). Feeding holes occur in trunks starting from ca. 5 m high and continuing up to ca. 10 m (Ramirez et al. 1977).

Captive animals accept grasshoppers (Orthoptera), wild bees (Hymenoptera), and moths (Lepidoptera); sometimes accept diurnal butterflies (Lepidoptera) and dragonflies (Odonata); and consistently reject mantids (Mantidae) and beetles (Coleoptera—Fajardo 1988). Crickets and small lizards (Anolis, Cnemidophorus lemniscatus, Gonatodes albogularis) are eaten head first (Fajardo 1988; Snowdon and Pola 1982). Although small snakes, poison arrow frogs (Dendrobates truncatus), and tree frogs (Hyla) are investigated, they are refused after smelling (Fajardo 1988). The pygmy marmoset will descend to the ground in pursuit of grasshoppers (Moynihan 1976a), and a captive pygmy marmoset stalked and killed a small passerine bird (Townsend and Wallace 1999).

Home ranges of pygmy marmosets typically include ca. 90 m of riverbank, with a 20–60-m extension inland (Soini 1988), and vary in size from 0.1 (Soini 1988) to 1.3 hectares (Castro and Soini 1977). Average home range size is 0.3–0.4 hectares (Ramirez et al. 1977; Soini 1988). Small home range sizes may be related to reliable exudate food sources (Ferrari and Lopes Ferrari 1989). About 10–40% of the home range is used more intensively than other areas and forms a core use area (Soini 1988). Within the home range, total horizontal movement averaged only 280–300 m per day (Soini 1982).

Callithrix pygmaea densities and home range sizes are influenced by predator and competitor population densities as well as availability of trees with exudate (Soini 1988). Arboreal ants are important competitors for exudate because they invade exudate holes, causing pygmy marmosets to sometimes abandon source trees (Soini 1988). Sympatric small primates who may compete with C. pygmaea for food include Saguinus fuscicollis, S. mystax, Callicebus moloch, Saimiri sciureus, and Aotus (Soini 1988). S. fuscicollis will chase pygmy marmosets away from exudate holes and could compete for exudate resources (Soini 1988). However, no aggression between these 2 primate species was observed while they fed on the same crown fruit of Ficus (Soini 1988). Squirrels, Microsciurus and Sciurus, use the pygmy marmoset's core area and infrequently feed from exudate holes (Soini 1988).

Core use areas may have fewer birds than surrounding areas, and pygmy marmosets actively chase flocking passerines and parakeets (Soini 1988). *C. pygmaea* may stalk small birds (Townsend and Wallace 1999) and family groups will mob nonvolant animals that move into their core areas. Species most often mobbed are snakes, squirrels, and humans, and those least often mobbed are tayras (*Eira barbara*), birds, and monkeys (Soini 1988).

Predators of *C. pygmaea* include ocelots (*Leopardus pardalis*), tigrillos (*L. tigrinus*), margays (*Leopardus wiedii*), jaguarundis (*Herpailurus yaguarondi*), and tayras. Overflying, perching, or alighting birds of prey cause pygmy marmosets to produce alarm calls, indicating these might also be potential predators (Soini 1988). Large climbing snakes such as the pit viper *Bothrops atrox* are probably important predators (Dixon and Soini 1977). Groups of pygmy marmosets produced alarm calls and froze when approached by capuchin monkeys (*Cebus apella*), suggesting that *C. apella* may be a predator of pygmy marmosets (C. H. Snowden, pers. comm.). Densities of these species are also inversely related, providing further evidence of a predator–prey relationship (Soini 1988).

Callithrix pygmaea may pollinate when they visit and systematically lap nectar from flower cups, as their muzzles are dusted with pollen (Janson et al. 1981).

Pygmy marmosets are too small to be hunted for food or bait and because they adapt to human-altered environments, they are probably in no danger of extinction (Freese et al. 1977; Mittermeier and Coimbra-Filho 1977). They are captured for pets by ringing the trunk of a large exudate-producing tree with resin, in which the animal becomes immobilized (Hernandez-Camacho and Cooper 1976).

Two of 8 (25%) pygmy marmosets examined from western Colombia were infected with *Trypanosoma* (*Schizotrypanum*) cruzi cruzi (Marinkelle 1982). Captive pygmy marmosets innoculated with varicella-zoster had low antibody responses and did not contract the disease (Asano et al. 1983).

BEHAVIOR. Callithrix pygmaea form 2 social units. Groups are cohesive and temporarily extended autonomous association of 2 or more individuals that may be accompanied 1 or more nonadults. Incipient associations are less cohesive, brief, or incipient associations of 2 or (less often) 3 individuals. In addition, individuals will forage, travel, and roost alone for at least several consecutive days (Soini 1988). Sixty-two percent of changes in group size were due to adult and subadult disappearance and reappearance, whereas 38% were due to recruitment, birth, losses, and mortality among juveniles and ambulatory infants (Soini 1988).

Group sizes range from 2 to 9 ambulatory individuals with 1– 2 carried infants (Soini 1982). The most common group size is 6– 7 (Moynihan 1976a; Ramirez et al. 1977; Terborgh 1983), but groups of 10–15 animals occur (Hernandez-Camacho and Cooper 1976). However, these larger groups may be aggregations of 2 adjacent, related groups (Soini 1988). Stability of social groups is related to reliability of exudate or available fruits in a given area (Ferrari and Lopes Ferrari 1989).

Individuals are monogamous and when caged in groups, only the dominant male and female breed (Christen 1968, 1974; Epple 1967, 1968). Also, births with surviving infants considerably alter and significantly delay both sexual behavior and ovulation in captive pygmy marmosets (Carlson et al. 1996).

In free-ranging troops, a dominance hierarchy is evident in feeding situations. A dominant male constantly follows an estrous female (Soini 1987). During this time, the male reduces time spent in insect foraging and infant carrying, while huddling and grooming time with the female increases (Soini 1987).

One source of exudate is used primarily by the dominant pair and their youngest offspring (Soini 1988). This dominant couple may restrict access to older offspring and force them to use secondary sources (Soini 1988). When the exudate yield of the principal tree declines, as may happen in the dry season in some portions of their range (Terborgh 1983), the group switches to the most suitable secondary source or may emigrate to a new site (Soini 1988).

Parenting duties are shared among all members of the family group (Soini 1988; Wamboldt et al. 1988). In captive studies, mothers carry new infants until about the 3rd week of life, at which time the male becomes the primary carrier with help from subadults and juveniles (Wamboldt et al. 1988). In the wild, at ca. 3 weeks of age, infants are carried by nonmothers, sometimes deposited in protected places such as exudate source trees, and watched over by siblings (Soini 1988).

Social grooming is an important aspect of the daily life of the pygmy marmoset (Christen 1974; Larsson et al. 1982; Ramirez et al. 1977). All group members participate and adults generally allogroom 9% of the day, but during postpartum estrus, allogrooming can increase to 20% of waking time (Soini 1987). Social grooming takes place during resting periods between late morning and early afternoon (Ramirez et al. 1977; Soini 1988). In captive studies, subordinate females groomed dominant females more times than they were groomed, males did not groom any particular female more than others, and females groomed males in about equal proportion

to being groomed (Christen 1974). Mothers consistently groomed infants more than did other members of the social group (Wamboldt et al. 1988).

Reproductive females become particularly intolerant and aggressive toward other group members during their 3rd month of pregnancy. This aggression often results in weaning of previous young and gradual ousting of subadults from main exudate source trees (Soini 1988). Peripheralization of subadults may begin when youngest siblings, still protected by their parents, chase them from the tree. Subadults then disperse and both sexes actively seek mates (Soini 1988).

About 32% of the pygmy marmoset's total daily activity is spent consuming and excavating for exudates, whereas foraging for insects takes up 16% of their time (Ramirez et al. 1977). The diurnal activity period lasts ca. 12 h (Soini 1982) and is regulated by photoperiod (Larsson et al. 1982). Pygmy marmosets begin to feed on exudates at 0540–0600 h and continue until 0630–0900 h when they begin to bask, huddle, groom, or play (Soini 1982). Insect foraging begins around 0900 h and a second rest period occurs in the early afternoon. Of total feeding time, 67% is focused on exudates and 33% on insect foraging. Most (75%) insect foraging is done within 5–15 m of the ground, 24% below 5 m, and only 1% above 15 m (Ramirez et al. 1977). Groups resume intensive exudate feeding about 1600 h and continue until they return to their roost at dusk (Soini 1982).

One animal usually calls the group and each member proceeds in single file, along a fixed customary path to the roost tree (Soini 1988). On at least 20% of evenings, calling occurs between individuals from opposite sides of the home range before all individuals finally move into the same tree (Snowdon and Hodun 1981). Members of the group usually roost together at a height of 7–10 m above the ground (Soini 1988). The roost may be a tree fork, a proximal part of a branch, or a stump from an old termite nest, and is not always concealed from view (Soini 1988). Almost all roosts are trees located at vegetation ecotones or water edges, with crowns disconnected from adjacent vegetation. Very rarely, pygmy marmosets use the main exudate tree for a night roost (Soini 1988).

Vertical clinging and leaping are the primary locomotory movements of *C. pygmaea* (Kinzey et al. 1975). Pygmy marmosets spend 77% of feeding time clinging vertically to exudate trees. Most (85%) of their leaps are either to or from a vertical position (Kinzey et al. 1975), although an animal may actually be resting upon an undetected horizontal protrusion (Soini 1988).

Callithrix pygmaea rapidly abandons social threat postures in response to images in a mirror (Eglash and Snowdon 1983). Pygmy marmosets locate otherwise unseen conspecifics in experimental mirrors and then threaten in the real direction, not in the mirror location (Eglash and Snowdon 1983). The capacity for mirror recognition indicates a high level of cognitive complexity in *C. pygmaea* (Eglash and Snowdon 1983). Other postures are described from captive studies (Christen 1968, 1974; Larsson et al. 1982).

Captive animals mark cages by depositing secretions from the urogenital region, abdomen, and sternum; males mark more frequently than females (Christen 1974; Larsson et al. 1982). In the wild, both sexes scent mark by pulling and rubbing leaves and stems between their legs especially during the postpartum estrus of the dominant female (Soini 1987).

Pygmy marmoset calls are higher than the frequency of the ambient noise with a frequency range that may be above the maximum auditory sensitivity of their major predators (Snowdon and Hodun 1981). Four trill variants are selectively used to either maximize or minimize detection. Pygmy marmosets use antiphonal calling. They can recognize each other on the basis of call structure, but recognition requires reinforcement when the tape is played from an animal's usual location (Snowdon and Cleveland 1980, 1984). Pygmy marmosets respond to a broad range of synthesized versions of their calls, but their responses differ when variants of these calls are used in different contexts (Snowdon and Pola 1978).

The trill variant that provides for sound localization over the greatest distance is referred to as a "j" call (Pola and Snowdon 1975; Snowdon and Hodun 1981). Pygmy marmosets approach exudate holes using a "j" call to announce their presence. Previously feeding animals either flee or return the "j" call to stop the approaching individuals (Snowdon and Hodun 1981). Young pygmy marmosets only use "j" calls, which may improve their chances of

being located by parents (Christen 1974; Snowdon and Hodun 1981).

Wild infants, juveniles, and subadults spend a considerable amount of time in both solitary play (acrobatic hanging, leaping, running, and imitative insect stalking) and social play (wrestling, biting, hide and seek, and ambush—Christen 1974; Soini 1988). Whereas adult play was not observed by Christen (1974), Soini (1987) saw adult play-chasing on days 14 and 17 postpartum.

GENETICS. Pygmy marmosets have 44 diploid chromosomes (Benirschke and Brownhill 1962). The Y chromosome is acrocentric and smaller than the medium-sized, metacentric X chromosome (Benirschke and Brownhill 1962; Egozcue et al. 1968a). Autosomes are categorized into 4 groups based on arm ratio and size (Seuanez et al. 1988). A clear sexual vesicle occurs in all cells before the meiotic division, but only in some spermatocytes and spermatids (possibly those with the X chromosome—Egozcue et al. 1968b).

The difference in chromosome number from the ancestral 2n = 46 (Hershkovitz 1977) may be because separation from the common stock occurred before differentiation of the Callithricidae (De Boer 1974 cited in Hershkovitz 1977). However the karyotype might have arisen from 1 similar to *Callithrix jacchus* through centric fusion of 2 pairs of small acrocentric chromosomes (Wohnus and Benirschke 1966). *Callithrix argenatata* shares 2n = 44 chromosome number with *C. pygmaea*, whereas *C. jacchus* has the same diploid number (2n = 46) as *Saguinus* and *Leontopithecus* (Seuanez et al. 1988).

Germ cell transfer between fraternal twins is possible because their placentas have interconnecting blood vessels (Wislocki 1939). Chromosomal chimera present in adult red bone marrow and testes of twins show this fetal interchange is operational (Benirschke and Brownhill 1962, 1963).

REMARKS. Hershkovitz (1977) describes *Callithrix* and *Cebuella* as closely related, but maintained *Cebuella* as a monotypic taxon containing only *C. pygmaea.* Moynihan (1976a) and Rosenberger (1981), noting the strong morphological similarities with other *Callithrix*, suggested changing the genus name. Groves (1989) agreed, viewing the pygmy marmoset as a paedomorphic derivative of the *C. jacchus* group. *C. pygmaea* is genetically closer to *C. argentata* than to *C. jacchus* (Porter et al. 1997; Schneider et al. 1996); both *C. argentata* and *C. pygmaea* differ from *C. jacchus* by 2 chromosomal characters (Barroso et al. 1997).

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