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# *Damonia crassiceps* Gray, 1870, a junior synonym of *Mauremys nigricans* (Gray, 1834) (Testudines: Geoemydidae)

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Gray (1870) described the turtle species "*Damonia* ? *crassiceps*" in his Supplement to the Catalogue of Shield Reptiles, which is part of his work on the chelonian specimens in the British Museum's natural history collection (now the Natural History Museum, NHM). The inclusion of a question mark in the binomial apparently indicated some uncertainty by Gray (1870) about the generic assignment of the species. He based the description solely on iconotypes, consisting of a series of three watercolor illustrations (Fig. 1a–c). These illustrations were bequeathed to the museum in 1835 by a British amateur naturalist, Thomas Hardwicke (1756–1835), as part of a large collection of zoological artworks. Although some chelonian illustrations from the NHM Hardwicke collection are available in print (e.g., Gray 1830–1835; Webb 1980), most were never published (Sawyer 1971). The physical specimen, from which the illustrations of *D. crassiceps* were created, has not been located (Iverson 2022) and likely was never deposited in a museum collection.

According to Gray (1870), Hardwicke acquired the three illustrations from another British amateur naturalist, John Reeves (1774–1856). While working for the East India Company in China, Reeves commissioned local artists to paint depictions of plants and animals (Fan 2004). In many instances, the artists produced multiple hand-drawn copies of each illustration. Reeves kept some of these for his personal collection and distributed the rest to other individuals and scientific institutions (Fan 2004; Datta 2018). Additional sets of Reeves' illustrations are held by the NHM Reeves Collection and the Zoological Society of London, ZSL (Sawyer 1971); both include examples of the illustration described as *D. crassiceps*. Based on the provenance of the illustrations received by Hardwicke, Gray (1870) designated the type locality of *D. crassiceps* as "China." However, the artists commissioned by Reeves often depicted captive specimens of exotic species not naturally found in China (Datta 2018), raising reasonable doubts regarding the accuracy of the reported type locality.

Smith (1931) placed *D. crassiceps* in synonymy with *Damonia subtrijuga*, a species initially described as *Emys subtrijuga* by Schlegel & Müller (1845). However, there is no evidence that Smith ever examined the original illustrations of *D. crassiceps* when making his assessment. Shortly thereafter, Lindholm (1931) recognized that *Damonia* was a preoccupied name and proposed the nomen novum *Malayemys*. Subsequent authors did not question the synonymization of *D. crassiceps* with *M. subtrijuga*, until Sumontha *et al*. (2016) challenged this arrangement. Gray (1870) described *D. crassiceps* as lacking lateral head markings, which Sumontha *et al*. (2016) noted are present in all known species of *Malayemys*. However, Sumontha *et al*. (2016) did not suggest an alternate taxonomy (TTWG 2021), and their publication did not meet the requirements for nomenclatural validity under the International Code of Zoological Nomenclature (Thomson & Lambertz 2017). See Dawson *et al*. (2020) for an extensive review of the complex nomenclatural history of *M. subtrijuga*. In recent taxonomic and systematic works, three species of *Malayemys* were recognized, with *D. crassiceps* remaining a junior synonym of *M. subtrijuga* (TTWG 2021; Iverson 2022). Determination of the correct identity of *D. crassiceps* is important, as it could potentially affect future chelonian taxonomy (TTWG 2021).

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In October 2018, FI accessed the unpublished volume of watercolors in the NHM Hardwicke collection and took high-resolution digital photographs of the three illustrations (numbered 19–21) used by Gray (1870) for the description of *D. crassiceps*. In December 2022, MB obtained additional photographs, including the corresponding duplicates of the illustrations in the NHM Reeves collection (plate 98) and the ZSL collection (plate 41). Using these images (Fig. 1), we confirmed and expanded the original description of *D. crassiceps*, established a putative species identification, and determined the sex of the depicted specimen through sexually dimorphic characters (tail morphology and coloration). To quantitatively evaluate our identification, we used ImageJ version 1.53a (Schneider *et al*. 2012) to measure the lengths of the right medial (inter-) seams between the pairs of gular (IG), humeral (IH), pectoral (IP), abdominal (IAB), and anal (IAN) plastral scutes in the ventral view illustration (e.g., Fig. 1c). For comparison, the same measurements were collected from live turtles and museum specimens and supplemented with published records (Iverson & McCord 1989; Ihlow *et al*. 2016). Measurements were normalized by dividing by the specimen's maximum straight carapace length (SCL). We performed a linear discriminant analysis on samples from the three currently recognized *Malayemys* species (*M. khoratensis*, *M. macrocephala*, and *M. subtrijuga*) and another Asian turtle species (*Mauremys nigricans*) and then *a posteriori* classified the illustration samples into one of these species groups using the lda() function from the package MASS version 7.3–61 (Venables & Ripley 2002) in R version 4.4.1 (R Core Team 2024).

*Museum acronyms*—FMNH = Field Museum of Natural History; MTD D = Herpetology Collection, Museum of Zoology, Senckenberg Dresden; NHM = Natural History Museum; THNHM = Thailand Natural History Museum; ZSL = Zoological Society of London.

*Material examined—Malayemys khoratensis*: 15 live specimens (Thailand) from the dataset of Ihlow *et al*. (2016); *Malayemys macrocephala*: THNHM 21364, THNHM 24984, THNHM 25295, and 48 live specimens (Thailand) from the dataset of Ihlow *et al*. (2016); *Malayemys subtrijuga*: 21 live specimens (Cambodia) from the dataset of Ihlow *et al*. (2016); *Mauremys nigricans*: FMNH 15902 and 11 live specimens (United States) from the dataset of Iverson & McCord (1989), MTD D 25623, MTD D 25624, MTD D 25684, MTD D 28456, MTD D 28484, MTD D 28989, MTD D 31851, MTD D 39157, MTD D 39795, MTD D 42496, MTD D 45358, 2 live specimens (China), and 3 live specimens (Germany). All handling of live animals for the current study was conducted in accordance with the policies of the Museum of Zoology, Senckenberg Dresden. Captive animals from private collections were examined with permission and remained the property of the respective owners.

*Expanded description of* D. crassiceps—Carapace oblong and slightly flared posteriorly; low domed and somewhat depressed, with an interrupted central keel; rear margin entire except for a distinct caudal notch; vertebral scutes broader than long; conspicuous growth annuli on each carapacial scute. Bridge with a single axillary scute and much larger inguinal scute. Plastron narrower than the opening of the shell; plastral formula: IAB > IP > IF > IG > IAN > IH; IP seam much (over 4X) longer than the IH seam; anal notch wide. Head very large and wide; eyes lateral; snout conical and projecting slightly; upper jaw unhooked and without a medial notch; tomia not denticulate. Legs covered in small scales, with larger oblong scales on the toes and anterior of the lower forearms; toes fully webbed. Tail moderately long; base wide; tapering to the tip; covered in numerous small scales dorsally, and larger square scales ventrally; cloacal opening near the posterior margin of carapace.

Coloration: Carapace brown, darker in areas of annuli, with dark central smudges on the vertebral and costal scutes; ventral side of marginals black in color, with multiple light-colored rays on each anterior scute, and a single broad triangular light ray in the center of each posterior scute. Bridge predominately black, with a bright red patch on each inguinal scute. Plastron horn-colored with irregular dark blotches on each scute. Top of head dark gray; iris light with dark spots around the reddish sclera; head entirely lacking any light-colored supraorbital, infraorbital, or nasal stripes, but with two fine cream-colored postocular stripes extending roughly parallel across the tympanic region and onto neck; jaws and chin reddish, with dark vermiculations and spots in front and below the eye and along the rear of the rhamphotheca; lower lateral side of the head stippled with faint cream-colored irregular spots; throat reddish with four dark streaks. Exposed portions of limbs mostly gray, with large dark red scales on the anterior of forelimbs; undersides and recessed areas of skin suffused with red.

The expanded description of *D. crassiceps* does not agree with the original description of *M. khoratensis* by Ihlow *et al*. (2016), the expanded description of *M. macrocephala* by Dawson *et al*. (2018), or the expanded description of *M. subtrijuga* by Dawson *et al*. (2020; Fig. 1d, g). However, several qualitative characters of *D. crassiceps* are useful in making a species identification, which is consistent with the expanded descriptions (Fang 1934; Iverson & McCord 1989; Anders & Iverson 2012) of *M. nigricans* (Fig. 1e, h; Table 1). The coloration of *D. crassiceps* matches Fang's (1934) "red phase" of *M. nigricans*, which was subsequently shown to be a sexually dimorphic character of adult males (Iverson

& McCord 1989; Anders & Iverson 2012). Based on this characteristic coloration and tail morphology (a wide base and cloacal opening near the posterior margin of the carapace), we conclude that the illustrated *M. nigricans* specimen was a male. Accordingly, we limited our quantitative analysis to male specimens, as relevant morphological characters differ between the sexes for this species.

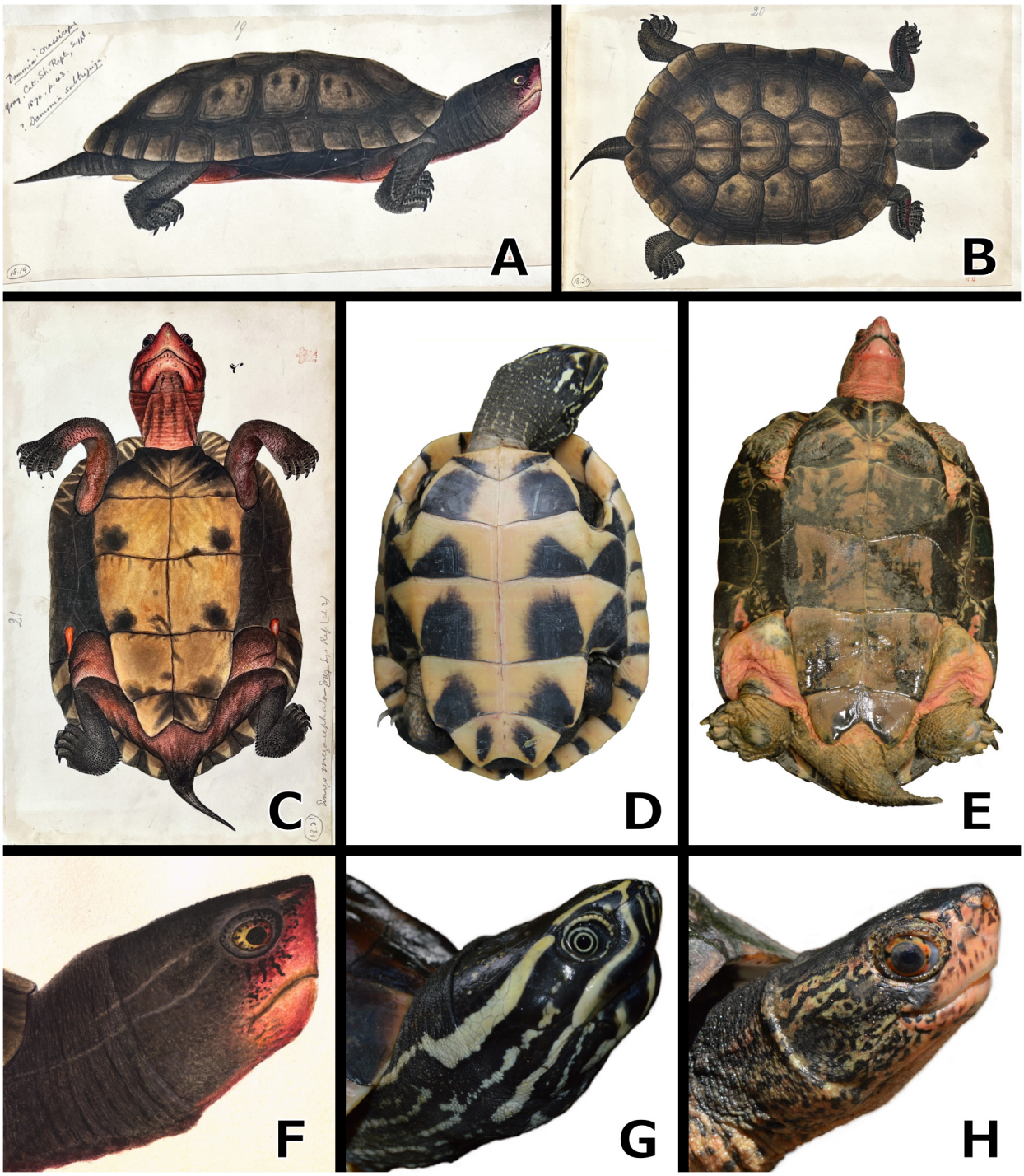


**FIGURE 1.** Comparison of the watercolor illustrations of *Damonia crassiceps* with other species: (A) lateral view of *Damonia crassiceps*, NHM Hardwicke coll. ill. 19; (B) dorsal view of *Damonia crassiceps*, NHM Hardwicke coll. ill. 20; (C) ventral view of *Damonia crassiceps*, NHM Hardwicke coll. ill. 21; (D) ventral view of *Malayemys macrocephala*; (E) ventral view of male *Mauremys nigricans*, (F) head of *Damonia crassiceps*, ZSL coll. plate 41; (G) head of *Malayemys subtrijuga*; and (H) head of male *Mauremys nigricans*. Photos not to scale. Credits: A–C from the collections of the Library and Archives, Natural History Museum, London. © The Trustees of the Natural History Museum, London; D by FI; E, G–H by JED; F courtesy of the Zoological Society of London, reproduced under a non-exclusive license, all rights retained by ZSL.

**TABLE 1.** Characters useful for comparing the illustrations of *Damonia crassiceps* to male *Malayemys* spp. and male *Mauremys nigricans*.

| Sample | N | red | stripes | ing/ax | IP/IH* | IF/IP* | IAN/IG* |
|---|---|---|---|---|---|---|---|
| *Damonia crassiceps* | 3 | present | fine (P C?) | long | 4.97 ± 0.56 (4.62–5.61) | 0.94 ± 0.00 (0.94) | 0.78 ± 0.01 (0.77–0.79) |
| *Malayemys khoratensis* | 8 | absent | distinct (S I N) | same | 1.40 ± 0.17 (1.20–1.67) | 1.16 ± 0.06 (1.08–1.25) | 0.93 ± 0.21 (0.71–1.25) |
| *Malayemys macrocephala* | 26 | absent | distinct (S I N P) | same | 0.96 ± 0.23 (0.67–1.86) | 1.55 ± 0.30 (1.13–2.08) | 1.10 ± 0.19 (0.72–1.65) |
| *Malayemys subtrijuga* | 13 | absent | distinct (S I N P) | same | 1.38 ± 0.21 (1.00–1.78) | 1.05 ± 0.16 (0.79–1.40) | 1.06 ± 0.10 (0.90–1.20) |
| *Mauremys nigricans* | 13 | present | variable (P C) | long | 2.53 ± 0.82 (1.49–4.68) | 1.09 ± 0.09 (0.92–1.26) | 0.83 ± 0.15 (0.54–1.09) |

*mean value, one standard deviation, and range (in parentheses).
red: red coloration of the head, throat, and limbs; stripes: pattern of stripes present on the head (S = supraocular; I = infraorbital; N = nasal; P = postocular; C = complex); ax/ing: relative size of the inguinal scute to the axillary scute (long = inguinal much larger than axillary; same = inguinal and axillary roughly equal in size); IP/IH: interpectoral seam to interhumeral seam ratio; IF/IP: interfemoral seam to interpectoral seam ratio; IAN/IG: interanal seam to intergular seam ratio.

In the linear discriminant analysis, the IP/IH ratio dominated the LD1 function (r = 0.88), while the IF/IP ratio was the greatest contributor to the LD2 function (r = 0.63), and the IAN/IG ratio had the highest influence on the LD3 function (r = 0.56; Table 1). The proportion of trace indicated that 86.6% of the among-group variance was explained by LD1, 11.4% by LD2, and 2.0% by LD3. The jackknifed accuracy of the analysis was 80.0%. The prediction of the linear discriminant analysis classified all three versions of the illustrations as *M. nigricans* (Fig. 2).

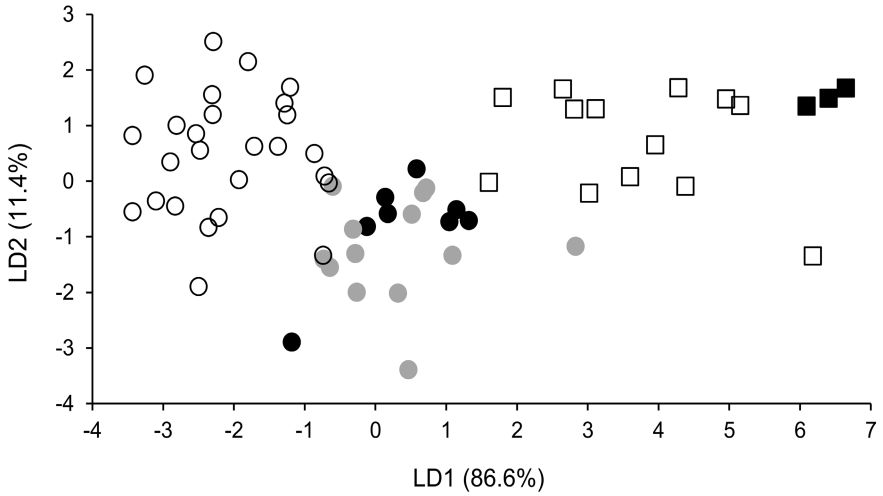


**FIGURE 2.** Plot of the first two functions in the linear discriminant analysis of the samples: solid black squares = *Damonia crassiceps*; solid black circles = *Malayemys khoratensis*; open circles = *Malayemys macrocephala;* solid gray circles = *Malayemys subtrijuga*; open squares = *Mauremys nigricans*.

Without a physical specimen, Gray's (1870) concept of *D. crassiceps* was hindered by small errors in the illustrations. In his description, he stated that the species lacked lateral head markings. However, the three versions of the illustrations exhibit some variation in this aspect. The illustrations in NHM Reeves collection plate 98 and ZSL collection plate 41 clearly display two fine postocular stripes, while the version available to Gray (1870), the NHM Hardwicke illustration number 19, shows only faint traces of these stripes. This discrepancy likely arose from the production of multiple copies by hand. In male *M. nigricans*, the narrow head stripes of juveniles typically become more complex with age,

often transforming into a vermiculated pattern of black, cream, and red (Anders & Iverson 2012). This pattern may be represented by the stippling on the lower lateral side of the head as seen in NHM Hardwicke collection illustration number 19 and ZSL collection plate 41 (Fig. 1f).

Another difference between the illustrations is the length of the IH seam. In our analysis, the IP/IH ratio was 5.61 in the NHM Hardwicke collection illustration number 21, but only 4.62 and 4.68 in the NHM Reeves collection plate 98 and ZSL collection plate 41. As with the head stripes, this discrepancy was likely the result of hand-illustrated duplications, and it is unclear which illustration most accurately depicts the IH seam length. According to Anders & Iverson (2012), the IP/IH ratio of *M. nigricans* averages 2.4 in males, but Iverson & McCord (1989) documented a specimen with a ratio of 4.26. In the present study, the highest IP/IH ratio in a specimen of *M. nigricans* was 4.68 (MTD D 45358). However, JED examined a specimen (not included in this study because shell damage precluded an accurate measurement) with an IP/IH ratio exceeding 5.0. Regardless, all *Malayemys* spp. have much lower IP/IH ratios (Table 1).

Our results show that the watercolor illustrations originally commissioned by Reeves do not represent *M. subtrijuga* or any other species in the genus *Malayemys*. Instead, comparisons with *M. nigricans* indicate that the illustrations depict an adult male of this species. First known as *Emys nigricans*, Gray (1834) provided a brief description of the species based on a nearly complete juvenile shell provided by John Reeves. Later, Gray (1844) offered additional details, but specimens of this species remained rare and were often confused with other species (Iverson & McCord 1989). Therefore, due to the insufficient material for comparison and the ontogenetic sexual dimorphism of *M. nigricans*, Gray (1870) described the illustrations that Hardwicke obtained from Reeves as a new species. Considering Gray's (1870) apparent doubt regarding the generic assignment of *D. crassiceps*, it is interesting to note that he also placed *M. nigricans* in the genus *Damonia* at the same time.

In conclusion, the nomen *D. crassiceps* is not applicable to any populations in the genus *Malayemys* and should be removed from synonymy with *M. subtrijuga*. Instead, *D. crassiceps* must be considered a junior subjective synonym of *M. nigricans*. As *M. nigricans* is native to southern China (Fang 1934; Iverson & McCord 1989; Anders & Iverson 2012; TTWG 2021), the type locality of "China" for *D. crassiceps* appears to be accurate. We surmise that the illustrated specimen was likely collected from Guangdong Province, in the vicinity of Guangzhou (formerly Canton) where Reeves was based. This area ("China prope Canton") is also the type locality for *M. nigricans* (Gray 1834).

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