

A REVIEW OF THE SOFTSHELL TURTLES OF THE GENUS *CHITRA*, WITH THE DESCRIPTION OF NEW TAXA FROM MYANMAR AND INDONESIA (JAVA)

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ABSTRACT.– Taxonomic, distribution and morphological data are presented for the trionychid turtle genus *Chitra* (Testudines: Trionychidae). Many confusing taxonomic details are clarified. Types and type localities are described for both previously named *Chitra* species. Details of forelimb scalation, chromatic and pattern characteristics, original head drawings accentuating phenotypic characters, shell morphology, general skeletal details, and mitochondrial and nuclear gene sequencing results are presented. The overall range of the genus *Chitra* is discussed, with details of field collections confirming previously undescribed Indonesian populations. A new species of narrow-headed softshell, *Chitra vandijki* sp. nov. is described from the Ayeyarwaddy River drainage, Myanmar, distinguished from its congeners by its distribution, a unique combination of carapace, head and neck patterns, and genetic sequence divergence of a level corresponding to full species recognition. A new subspecies of narrow-headed softshell turtle, *Chitra chitra javanensis* ssp. nov., is described from eastern Java, Indonesia, distinguished from the nominate subspecies by its distribution, by details of carapace, dorsal head and chin patterns, and by a genetic sequence divergence level appropriate to subspecies status. Lastly, a first-use chresonymy is presented for the genus *Chitra* and included species.

KEYWORDS.– Testudines, taxonomy, systematics, Trionychidae, *Chitra*, Ganges, Ayeyarwaddy, Mae Klong, Pasuruan.

BACKGROUND *CHITRA INDICA*

During much of the Nineteenth Century, the spoils, trophies, and curiosities of the British Empire flowed from the far corners of the globe into London, the hub of the entire colonial enterprise. Among these items, little noticed at the time, were both some original paintings and a preserved specimen (having died *en voyage*) of a truly extraordinary turtle from India. These miscellanea gave tangible evidence of the existence of a giant Asiatic softshell turtle with a remarkably small, narrow head, and eyes so small and far forward that many biologists, seeing a skull, are inclined to mistake the orbits for the nostrils.

The evidence for this strangely proportioned creature's existence specifically included a pair of water-colours painted for Major-General

Thomas Hardwicke (1755-1835), who employed both Indian and British artists (Archer, 1962; Wheeler, 1998). These were completed while Hardwicke was in the service of the East India Company, commanding the Bengal Artillery. They were brought to England when Hardwicke retired in 1823, and he bequeathed them, along with various other turtle paintings, and several hundred drawings of other Indian reptiles and amphibians, to the British Museum of Natural History (= BMNH) upon his death in 1835 (Dawson, 1946). Another Englishman in service in India was Dr. Francis Buchanan-Hamilton (1762-1829), who at different times, was supervisor of both the "Calcutta Garden" (now the Alipore Zoological Gardens, Kolkata) and the "Institute for Promotions of the Natural History

of India” (“The Barrackpore Menagerie”) where actual specimens were documented by “careful drawings” (Archer, 1962). Basically, the two men worked in a cooperative spirit, sometimes having their staff copy paintings in each other’s collections. Today, these originals of Hardwicke’s “coloured drawings” reside in bound volumes in the Zoological Library of the BMNH in London, and those of Buchanan-Hamilton in the India Office Library, also in London (Webb, 1980; Wheeler, 1998). Other artistic works from Hardwicke and Buchanan-Hamilton are thought to have been deposited with the East India Company, or with the Library of the Asiatic Society of Bengal, but cannot now be traced (S. Biswas, pers. comm. to Webb, 1980).

Hardwicke’s surviving turtle drawings, thirteen in number, bear BMNH identification numbers 28 to 40. The illustrations of the new, giant softshell turtle, numbers 31 (dorsal) and 40 (ventral), bear the handwritten inscription “Sewteree – Country Name Found in the Ganges – grows to the size of 240 lbs. Futtehghur May”. The illustrations themselves are well done and clearly show the four plastral callosities; the small, very narrow head with short nasal tube; the extraordinarily small, anteriorly located eyes; the longitudinal lines on the neck; the paramedian neck lines forming a “V”; the complex, vermiform marbling of the leathery shell; and the concave posterior border of the bony carapace that together characterize the genus *Chitra*.

Hardwicke also collected specimens, but all three collections that he shipped to London were lost by shipwreck (Gray, 1872). Nevertheless, it appears that one narrow-headed softshell specimen, reportedly from the East Indies, did reach London safely, although it cannot be located today (Farkas, 1994: 117). This was received in a fluid-preserved state by the Royal College of Surgeons (= RCS), where in 1817 (Farkas, 1994: 118) it was listed in the “Rough Minute Book” of the College as “No. 903 [= ledger or entry #]. Mr. Henderson. East Indies. Sept. 4th 1818. A specimen of the soft shell’d tortoise, called ‘mud-tortoise.’ (Brought by the General Kyd Indiaman,

and died on its passage.) *Testudo membranacea*. Nat. Hist. [specimen] No. 1238.B.”

The name *Testudo membranacea* was first used by Blumenbach (1779) with the clearly erroneous type locality “Guiana” (living trionychids are unknown in South America), and was considered (e.g., by Wermuth and Mertens, 1961, 1977) to be a questionable synonym of *Testudo cartilaginea* Boddaert (1770), which was the first trionychid turtle to be described. Both names describe general qualities of all trionychids, i.e. the seemingly non-bony, cartilaginous or membrane-like shell. It is uncertain what actual species was represented by the name *T. membranacea*. No type was designated. Gray (1831b) did not clarify the matter when he placed it (with question) in the synonymy of the African *Trionyx Niloticus*, which in itself was an unjustified replacement name for the older name *Testudo triunguis* Forskål (1775). We hereby declare the name *Testudo membranacea* a *nomen dubium* for the reasons stated above (see also chresonymy).

A later entry, by Richard Owen in an 1859:104 RCS catalogue, reads: “No. 685 [ledger #]. The Indian Mud-Tortoise (*Trionyx indicus*, Gray; *Testudo membranacea*, Henderson). Fig. Gray, *Illust. Ind. Zool.* vol. i. p. 80. *Cat. of Tortoises in Brit. Mus.* p. 49. Hab. Penang. [= same basic locality as RCS “Nat. Hist. No. 1238.B” (= RCS 1238.B)] Presented by Dr. Henderson.” (Farkas, 1994: 117). This specimen is also presently unaccounted for and is likely the same (RCS 1238.B) specimen as is mentioned in the 1817 Royal College of Surgeons ledger “No. 903”.

J. E. Gray (1800-1875), the prolific chelonian (among other topics) specialist at the British Museum (BMNH) for much of the 19th century, reproduced some of Hardwicke’s and Buchanan-Hamilton’s paintings (see Archer, 1962) in his oversized folio “*Illustrations of Indian Zoology*,” a two volume work, comprised of 202 colored plates, originally produced as 16 issues in 20 parts (Wheeler, 1998) between 1830 and 1835. Although Hardwicke provided most of the illustrations and financed the work, Gray ed-

ited and described the new species illustrated [with a few exceptions credited to Bell (1829-1842) by Bourret (1941: 158) and Wheeler (1998: 349), plus see "T. Bell" in Iverson (1992: 166), but we agree with Boulenger (1889), Wermuth and Mertens (1961) and Iverson (1992), crediting the contested species to Gray (1831b: 20, 21, 23) being first published], so this work is attributed solely to Gray (Wheeler, 1998: 348). The accompanying text, the "*Prodromus Faunae Indicae*" was never published, as explained by Dawson (1946: 63). Plate 80 (Fig. 1), copied as a composite of Hardwicke's paintings (BMNH 31 and 40) of the narrow-headed softshell species, is thought to have been published in October of 1831 (Kinnear, 1925; Sawyer, 1971; Webb, 1980; Wheeler, 1998), and is identified in the second of two unnumbered introductory pages as "Egyptian Trionyx. *Trionyx Aegyptiacus*, var. Indica" (see *Trionyx Aegyptianns* [sic] in Appendix). The actual caption to the plate itself is slightly different: "TRIONYX AEGYPTIACUS. Var. Indica. n. EGYPTIAN TRIONYX. Indian. Var. Ganges, called Sewteree, sometimes grows to 240 lbs." The contemporary Hindi and Bengali vernacular words for the species today are both "Chitra", not "sewteree," although the latter name lives on in the label of a small stuffed ("young") specimen (see Boulenger, 1889: 265, specimen "b", Capt. Boyes) of this species from "India" in the BMNH 48.2.1.39 (see also Boulenger, 1889: 265 (BMNH 48.8.14.11), "Hgr." (half grown) specimen "a"). It should be noted that, in pre-Partition days (i.e., pre-1947), the term "India" was an inclusive one, including present day Bangladesh, Pakistan, sometimes Burma (Myanmar), as well as the present Republic of India.

Gray had described the narrow-headed softshell more formally in two prior publications (Gray, 1831a, 1831b). The first of these descriptions makes no mention of a type specimen, although it does refer to the author's *Illustrations of Indian Zoology*, but without mention of Hardwicke. However, the second description specifically associates Hardwicke, and thus his two paintings (BMNH 31 & 40), with the au-

thor's *Illustrations of Indian Zoology* and clearly refers (although without quoting catalogue number) to an actual specimen deposited in the RCS collection. This would be the Henderson specimen (RCS 1238.B) alluded to above, which is presumed destroyed by wartime bombing in 1941 (E. Allen, pers. comm. to Farkas, 1994).

The actual wording of Gray's two brief descriptions is as follows:

Gray 1831a, p. 18: "*Indian Trionyx. Trionyx Indicus*, Gray, *Illust. Ind. Zool. t.* Olive green, with black-edged, irregular pale tortuous and forked streaks; sternal callosities four, the hinder ones rounded triangular. India."

Gray 1831b, p. 47: "*Trionyx Indicus*, (*Indian Trionyx.*) – Testa supra subconvexa olivaceo viridi, lineis irregularibus tortuosis vel furcatis nigro marginatis ornata, sterno 4-callosa, callis lateralibus quadrangularibus, posticis longe triangularibus, cauda brevi.

Trionyx Aegyptiacus, Var. [sic] *Indicus*. Hard. *Illust. Ind. Zool. T. Testudo Chitra*, Hamilton, *Icon. Ined.* (v. *Icon. Mus. Ind.*)

Habitat. In India, fl. Ganges, Penang, *Dr. Henderson*, (v. *Mus. Col. Surg.*)

Sometimes weighing 240 pounds. The lateral callosities are four-angular, and of nearly equal width at each end; their inner extremity is obliquely truncated in front; the hinder callosities are parallel, long triangular, with the outer side slightly rounded."

As explained by Webb (1980: 70), Gray (1831a) appears to have been published before Gray (1831b). Most authors (see Farkas 1994) over the last century have considered the more detailed Gray (1831b) to be the source of the new name *Trionyx indicus* [now *Chitra indica*] with its declared type specimen and explicit citation of the Hardwicke drawings (Plate 80) in Gray's *Illustrations of Indian Zoology*. For reasons of precedence and taxonomic stability we hereby clarify that Gray (1831a) is the original description of *Chitra indica*.

As stated, Hardwicke retired and returned to England in 1823 at the age of 67, after which he spent time at the BMNH and exchanged notes with Gray in the ensuing years (including the unpublished "*Prodromus Faunae Indicae*"), so that

Gray would have had access to the Indian softshell paintings before they were bequeathed to the British Museum of Natural History in July of 1835 (Dawson, 1946: 60), allowing him to publish copies of them in 1831.

Gray explicitly indicates that he had access both to Hardwicke's paintings and to the Henderson specimen in the RCS when he wrote his 1831 descriptions. He also had obviously seen the unpublished painting ("Icon. Ined.") of Buchanan-Hamilton's *Testudo Chitra*, which he correctly associated with the Hardwicke and Henderson material. An actual cited specimen co-existing with cited illustrations at the time of description has precedence over the illustrations when it comes to the designation of type material. We will not disagree with Farkas (1994: 117) that the RCS (#1238.B i.e., Henderson's) specimen "could" be considered a syntype of *C. indica*, but since it is the only actual specimen on which the species was based, we feel it should be considered the holotype, which in turn requires the designation of a neotype to clarify the taxonomic status of *Chitra indica* in view of the apparent destruction of this holotype during World War II. The specimen illustrated on Gray's plate 80 in the *Illustrations of Indian Zoology* (1830-35), upon which Gray's (1831a) original description of *C. indica* is based, could itself be a neotype, in that it was not published until 19 October, 1831 (Kinnear, 1925; Webb, 1980), whereas Gray's (1831b) description utilizing the now lost RCS #1238.B specimen as its type appeared earlier in 1831 (Webb, 1980). In agreement with Webb (1980: 64), we hereby recognize the specimen illustrated on Plate 80 (a composite of Farkas's, 1994 iconotypes BMNH 31 and 40) of Gray's *Illustrations of Indian Zoology* (1830-35, Vol. I, part 8) to be the neotype of *Trionyx indicus* Gray (1831a: 18) [= *Chitra indica*]. Although not perfect, Plate 80 displays diagnostic characters of *Chitra indica* such as its head, neck and carapacial markings, and the presence of four lamellae and three pseudodigits on the forelimb (see Figure 1, Table 1).

The current version of the Code of Zoological Nomenclature (ICZN, 1999) specifically permits the use of an illustrated individual as a type

specimen: Article 73.1.4: "designation of an illustration of a single specimen as a holotype is to be treated as designation of the specimen illustrated; the fact that the specimen no longer exists or cannot be traced does not of itself invalidate the designation."

The above historical points have interesting implications, one being that the suggested type locality of *C. indica* has varied from "Found in the Ganges... Futttehghur, May" as inscribed on Hardwicke's BMNH 31 and 40 illustrations, to "East Indies" for Hardwicke/Henderson's RCS specimen #1238.B, to "India" (Gray, 1831a), "In India, fl. Ganges, Penang" (Gray, 1831b), "Ganges" as given on Gray's (1831) Plate 80, or "Fatehgarh, Ganges" by Smith (1931). [Not restricted to "Barrackpore" India as stated by King and Burke (1989: 110, see Webb, 1980: 61; Archer, 1962: 39; Iverson, 1992: 310.)] If one were to focus on Gray (1831b), historically although incorrectly often cited as the original description (see above), and assign the Penang locality to Dr. Henderson's "v. Mus. Col. Surg." (RCS #1238.B) specimen, this might suggest Penang (Malaysia) as the type locality of the only actual specimen upon which *C. indica* was described. However, accepting Gray (1831a) as the original description removes this confusion, since that reference cites "India" for the locality. In addition, the specimen illustrated on Plate 80, the neotype, records "Ganges" as the locality. Various authors cast doubt upon the "Penang" possibility, including Farkas (1994), who observed that the species "is not known to occur at Penang (Malaysia)," and Smith (1931) who doubted the validity of some of T. E. Cantor's Penang, Malaysia collection data. Nevertheless, this paper will later demonstrate that a Penang, Malaysia locality is not impossible for this genus.

Smith (1931: 162) selected "Fatehgarh [a modern transliteration of the word Futttehghur, a Hindi town name taken from the actual locality written in Hardwicke's paintings], Ganges" as the type locality, on the grounds that Hardwicke conducted at least some of his documented collecting activities there. This is in agreement with the locality "India" given in Gray (1831a), the original description, and "Ganges" given for

both Hardwicke's paintings and the specimen illustrated on Plate 80, the neotype of *C. indica*. Unfortunately, after Hardwicke died, legal problems arose concerning the text and money that he had set aside to allow Gray's ongoing *Illustrations of Indian Zoology* project to include his (Hardwicke's) personal data as the "*Prodromus Faunae Indicae*." While some of Hardwicke's notes were "placed in chancery" (i.e., confiscated by the court), where they remained a century later (Smith, 1931), the manuscript of the "*Prodromus Faunae Indicae*" remained in Gray's possession until 1873, when he apparently burned it (Dawson, 1946: 63). We hereby agree with Smith (1931) as first reviser, and Webb (1980), accepting "Fatehgarh on the river Ganges, India" as the type locality of Gray's (1831a: 18) *Trionyx Indicus* [= *Chitra indica*].

There is also the question of Buchanan-Hamilton's *Testudo Chitra*, a taxon based upon painting #522 of the India Office Library and Records Department, London (see Webb, 1980: 67). The species name was based upon the widespread Hindi vernacular name for the species, which in turn derives from the Bengali word for "picture," an allusion to the distinctive carapace design. This combination was never actually published as a valid name, having been merely a handwritten caption on an unpublished artistic rendering until Gray (1831b) placed it into synonymy with *Trionyx Egyptiacus*, *Var.[sic] Indicus*. Further, Wermuth and Mertens (1961, 1977) declared *Testudo chitra* to be a *nomen nudum*. Nutaphand (1986, 1990) chose this same specific epithet for a valid new species of narrow-headed softshell from Thailand (i.e., *Chitra chitra*), and may therefore have revalidated it (see below).

Subsequent manipulations of the nomenclature involving *Chitra indica* (commonly called the "Narrow-headed" or "Giant" Indian Softshell) include the division by Duméril and Bibron (1835) of the trionychids into those with fleshy valves or flaps under which the posterior limbs could retract (Cryptopodes), and those in which these valves are absent (Gymnopodes). This was a justified division, and corresponds to the modern subfamilies Cyclanorbinae and

Trionychinae (e.g., Meylan, 1987). In Duméril and Bibron's system, this giant Indian species fell into the second category, and was named *Gymnopus lineatus*, based upon a specimen in the Museum national d'Histoire Naturelle, Paris (= MNHN) collection from the Ganges and presented by Dussumier de Fombrune. This new specific epithet, only conditionally being considered the same as *T. indicus* (see Duméril & Bibron, 1835: 493), with a description based on its own type (MNHN 6968) and locality ("le Gange"), is not a replacement name (*nomen novum*), but a subjective synonym of *T. indicus*, and therefore must be treated as a separate name rather than a *nomen novum* or a *nomen substitutum* for *T. indicus* (see Bour et al., 1995: 82).

Gray elevated *T. indicus* to its own genus, as *Chitra indica*, in his 1844 Catalogue, although his brief and imprecise description, with its mention of "Head very depressed, large, dilated behind. Muzzle very short [and] broad" and "head olive, minutely black-dotted", and above all, the occurrence in the "Philippine Islands", leads to the conclusion that he had before him specimens ("a" and "b") of what was later to be designated as *Pelochelys* (see syntypes of *P. cumingii* in Appendix), and not *Chitra*. But he did equate the species (*Chitra indica*) with his earlier (thus having priority over *Pelochelys*) name *Trionyx indicus* and with Buchanan-Hamilton's *Testudo Chitra*, and it is best to conclude (as did Wermuth and Mertens, 1961) that the generic description was a composite of both *Chitra* and *Pelochelys*. Much later, Gray (1864: 91) downplayed the significant differences between the two genera as follows: "This genus [i.e., *Chitra*] and *Pelochelys* are so similar externally, especially in the dried or stuffed specimens, that the specimens were named alike in the British Museum, and so remained for years, though in the meantime they had been examined by several herpetologists, both English and foreign. It is only by a slight difference in the length of the head, compared with the width and the flatness and slight convexity of the forehead, that they can be distinguished, different as the forms of the skulls are." Boulenger (1889: 263) clarified matters to some

degree, redefining Gray's genus *Chitra* and providing excellent engravings of the different skulls of the two genera. However, he too, perpetrated an inconsistency by stating that the range of the genus *Chitra* was "East Indies," whereas that of its only known species, *C. indica*, was given as "Ganges and Irawaddy."

The generic designation *Chitra* Gray (1844) prevails over *Gymnopus* Duméril and Bibron (1835) because *Gymnopus* is a substitute name for *Aspidonectes* Wagler (1830), both having the same type species (i.e., *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, 1809, [= *Trionyx triunguis* (Forskål, 1775)] by subsequent designation of Fitzinger, 1843: 30; see Bour et al., 1995: 79). Moreover, *Gymnopus* Duméril and Bibron (1835) is preoccupied by *Gymnopus* Brookes (1825, Aves), and is thus an invalid junior homonym. For reasons given above, and for taxonomic stability, we accept *Chitra* as the appropriate genus for Hardwicke's, Buchanan-Hamilton's, Henderson's, Duméril and Bibron's, Smith's and Gray's drawings and specimens discussed above, with *Trionyx indicus* Gray, 1831a [= *Chitra indica*] as generotype, and "Fatehgarh on the river Ganges, India" as the type locality for the first described species.

CHITRA CHITRA

A second species of *Chitra*, from western Thailand, was mentioned by Nutaphand in 1986, and formally described a few years later (Nutaphand, 1990). The brief account was published in the Thai language, and translates as follows:

Ta Pab Manlai, Griu Lai, Grau Daung.
Kamburien [sic] Giant Soft-shelled Turtle
Chitra chitra, Gray [sic].

The Kanburien Giant Soft-shelled Turtle is a very big species, the biggest softshell in the world. Among the Chelonia the only species with a greater carapace length is the Leatherback Turtle (*Dermochelys coriacea*), which is a marine turtle and not a softshell.

This species occurs in the Mae Klong in Ratburi [Province] and Khwae River in Kanchanaburi [Province]. Adults have a carapace

length of up to 100 cm and a length to 140 cm, and a weight up to 120 kg.

Dorsal carapace colour is faded brown or yellow-brown, with irregular pale brown markings. The pattern varies somewhat between individuals. The neck bears five lines, and the posterior end of the carapace shows variable ornamentation resembling a [military] camouflage pattern. The ventral surface tends to be pinkish-white.

There are two species. The species found in Thailand has characteristics as described above. The Thai turtles are larger than those from India, having a pale but very bright colour, and should therefore be called *Chitra chitra*; those in India are small and have a carapace colour that is mid-olive, and these are named *Chitra indica*.

This description barely meets the criteria for a species description according to the Code of Zoological Nomenclature, and no type specimen is indicated, although there is no doubt that Nutaphand's intent was to describe the Thai form as specifically distinct from that on the Indian subcontinent.

It is not certain why Nutaphand (1990: 103) used the specific epithet *chitra* and attributed his species *C. chitra* to Gray. Because Nutaphand has not responded to our inquiries, as next reviewer we offer the following likely explanation. We accept that Nutaphand's first exposure to the name "*chitra*" was in Gray's description of the genus *Chitra* in 1844 (thus the credit), and in that same publication Gray (1844: 49) he also saw the *nomen nudum* *Testudo Chitra* (see below). Without mention of "B. Hamilton" or "*Testudo Chitra*" he apparently decided to resurrect "*chitra*" as a species name for his new form, *Chitra chitra*.

In light of Nutaphand's description, the status of Buchanan-Hamilton's and Gray's (1831b, 1844) *Testudo Chitra* must be discussed further. Wermuth and Mertens (1961, 1977) declared "Hamilton's" *T. chitra* a *nomen nudum*, a position with which we agree. Webb (1980) declared *T. chitra* Gray an unavailable name (unpublished by ICZN Code Standards). We agree with Webb that *T. chitra*, published first in Gray (1831b) only as a synonym, does not qualify as a proper

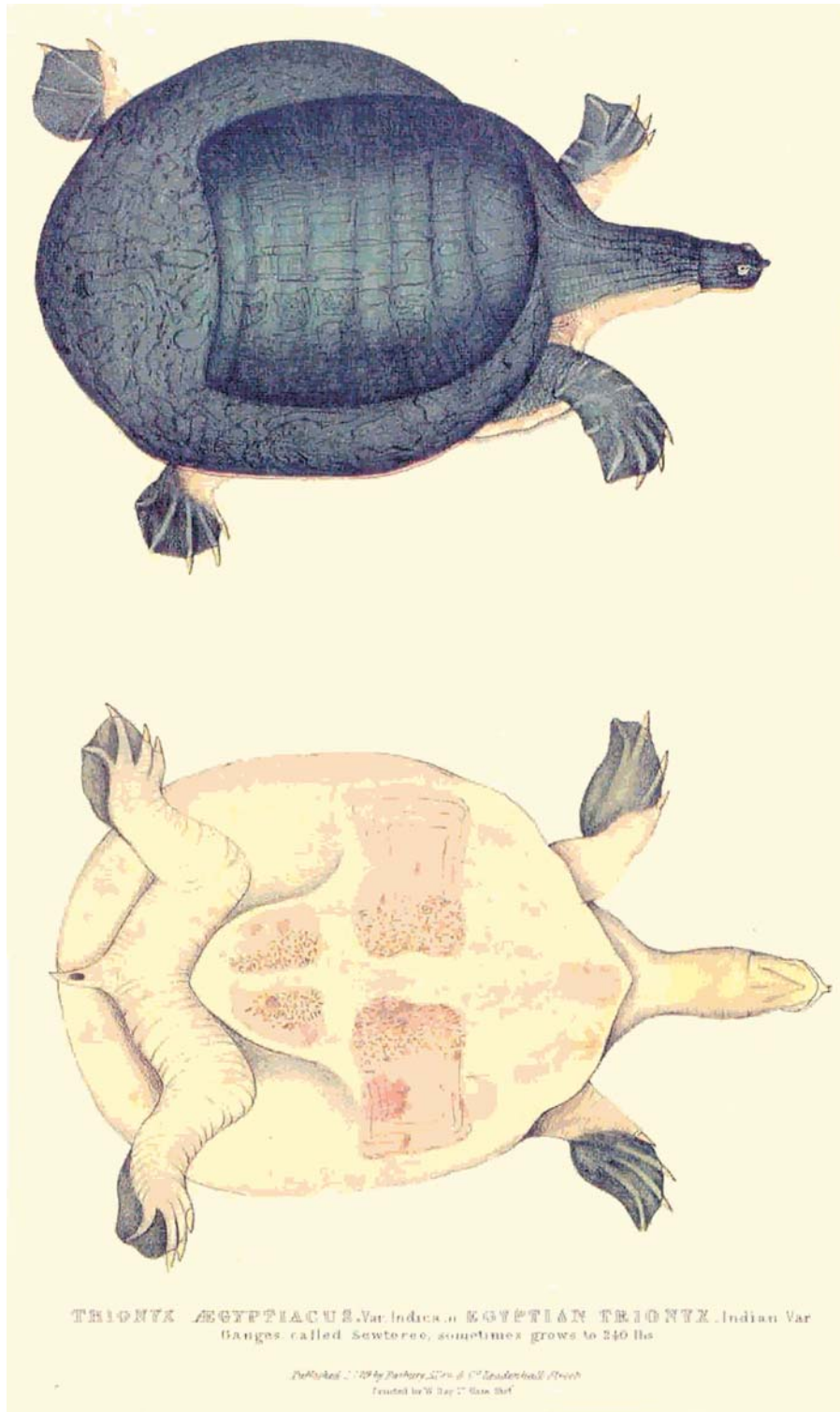


FIGURE 1: Plate 80 in *Illustrations of Indian Zoology* (Gray, 1831 ["1830-35"]).



FIGURE 2: Illustration of *Chitra chitra* specimen presented in Nutaphand (1990:104).

description; however, Nutaphand (1990), has again used the specific epithet “*chitra*” for a new taxon, making it now an available name.

Nutaphand (1990) did not designate any type specimen in his original description of *C. chitra*, although he did present an illustration. To clarify the taxonomic status of *C. chitra*, we feel it best to now designate type material that is in agreement with Nutaphand’s original description. Since the best example of *C. chitra* documented by Nutaphand himself is the photo given on page 104 of his original 1990 description, in the absence of any designated type material, we herein designate the specimen illustrated in this photo (Fig. 2) as the holotype of the species *Chitra chitra* (see the same photo labeled *C. indica*, as Figure 127, page 160 in Nutaphand, 1979). This illustration displays features herein attributed to Nutaphand’s *C. chitra* such as a “simple” carapacial pattern, a continuous pale rim on the carapace, a neck “V” located near the base of the neck, and the presence of a nose/eye “triangle” figure (see description of *C. chitra* below for more detail).

Nutaphand also did not specifically designate a type locality, but he did give two general localities (see above) where *C. chitra* was to be found. We therefore designate Kanburi (presently Kanchanaburi), where the Khwae Noi and the Khwae Yai rivers join to form the Mae Klong River in Kanchanaburi Province, Thailand as the type locality of *Chitra chitra* (see Smith, 1922, 1930, 1931).

GEOGRAPHIC DISTRIBUTION OF THE GENUS *CHITRA* (FIG. 3A)

Much of the turtle literature of both the 19th and 20th centuries has suggested that the distribution of the genus *Chitra* is restricted to the Ganges (today called Ganga) system in northern India (now including Bangladesh) and adjacent Nepal (e.g., Gray, 1864). However, Gray’s (1831b) mention of a specimen from “Penang”, suggested that the range is much wider than generally thought. Subsequently, Smith (1931) confirmed that the genus occurred in western Thailand; and Webb (1981) documented two specimens (ZSI 21539, n= 2) “from Dhond, (about 190 km ESE Bom-

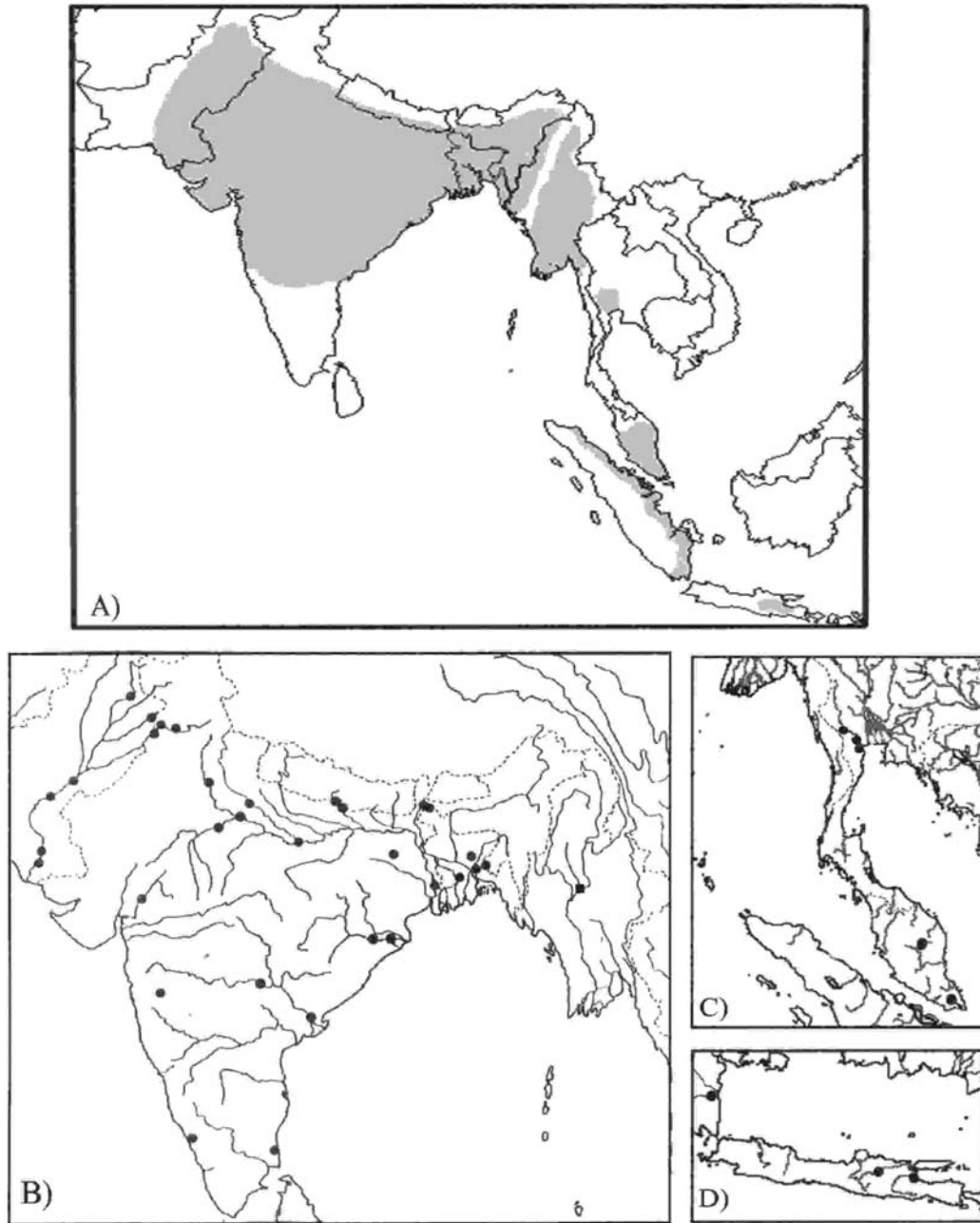


FIGURE 3: Distributions of the species and subspecies in the genus *Chitra*, generally taken from Iverson (1992), but including data from field notes (see text): (A) Overall *Chitra* distribution; (B) *C. indica* (dots) and *C. vandijki* (square); (C) *C. c. chitra*; (D) *C. c. javanensis*.

bay), in the State of Maharashtra”, India. Das (1991) recorded *Chitra* from various river systems in peninsular India, including the Mahanadi, Godavari, Krishna, and Cauvari systems. Minton (1966, pl. 11) illustrated a live adult (now AMNH, 85594) from the “Indus River, near Tatta, Tatta District, Pakistan”, and noted that, in Pakistan, it appeared to be restricted to sandy sections of the Indus and other large rivers. In 2001, one of us (WPM) received five live specimens, also from Pakistan (see below).

Das (1995) summarized the distribution of *C. indica* in Bangladesh, India, Nepal and Pakistan. Furthermore, Rashid and Khan (2000) reported that *C. indica* is found in all the major rivers of Bangladesh and their major tributaries. They also noted that it has become rare in the northeast, northwest and central regions, and is uncommon in the southern districts. In Nepal, Shrestha (1996a, b) reported populations of *C. indica* in the Patharbhoji section of the Grewa River, and considered it to be one of the most common species in the Karnali area. Overall, the species was described as locally common in suitable habitat in Nepal.

These records indicate a wide distribution of *C. indica* throughout the Ganga and Indus river systems, as well as in various rivers of peninsular India (see Fig. 3B). We have, at present, no indications of significant geographic variation in *Chitra* within the Indus-Ganga-Brahmaputra River systems or the smaller river systems of peninsular India, apart from the casual observation of Rashid and Khan (2000) that, in Bangladesh, individual *C. Indica* from the northern and central areas are lighter in colour than those from the south.

Myanmar.-The genus *Chitra* is not included in the recent account by Platt et al. (2000) of tortoise and turtle exploitation in Myanmar. Smith (1931) wrote: “It is said to inhabit the Irawaddy, but I cannot trace any specimen having been obtained there.” In 1868 Theobald also did not record *Chitra* in “Birra”, but later listed them in 1876, and in 1882, even going as far as calling Burmese *Chitra* “savage and dangerous creatures”.

Additional hints of the occurrence of *Chitra* in Myanmar have circulated since the statements of Boulenger (1889), Siebenrock (1909), and Annandale (1912), that *Chitra* was to be found in the “Irrawaddi” or in “Burma”, and recent comments by van Dijk (1994) lend substance to this. There is an adult *Chitra* specimen (BMNH 87.3.30.11) bearing the Museum label “Ad. skel. Allahabad. Exch: -w. Theobald Esq. Incomplete” and cited with similar data by Boulenger (1889:265) as specimen “d”, that is likely the basis for Boulenger’s “Irawaddy” *Chitra* record. There is also a juvenile trionychid, deposited by W. Theobald in the BMNH collection (# 87.3.30.15), labeled “*Pelochelys cantoris*” (see Boulenger (1889:263) specimen “c” from “Burma”; see also Appendix). This specimen is small and consists mostly of the bony carapace (bony disc 7 x 7 cm), and although areas of the leathery carapacial flap are present, they are, at this time, purely black in colour, with no evidence of pattern. The specimen appears, by morphology (see below) to be a *Chitra* rather than a *Pelochelys* (examined by PCHP), but the distinctive markings of the “Burma” form (see below) are no longer in evidence.

Van Dijk (1994) provided the first precise records from Myanmar: a bony trionychid carapace from the Man River, a carapace and plastron from the Mon River, and a partial plastron from the Doke-tha-wady. Careful examination of key characters, including the angled form of the hyo-hypoplastral suture, the relationship between the first and second rib-tips, and the overall form of the rib tips projecting beyond the bony carapace margin, led van Dijk (1994) to the conclusion that the specimens were *Chitra* and not *Pelochelys*.

Subsequently, specimens have been obtained by Yuk Wah (Oscar) Shiu of Hong Kong from the market in Ruili, Yunnan, China, extremely close to the Myanmar border, and the conclusion has been reached (e.g., by Kuchling, 1995, who examined turtles in the same market) that the turtles sold there came from adjacent parts of Myanmar. Four of these specimens have been catalogued into the Chelonian Research Institute

(CRI) collection (PCHP 4896, 4897, 5050, 7059).

More recently, a live Myanmar *Chitra* with precise collection data was reported by Platt (2001). This specimen, a subadult with total carapace length (CL) of 40.8 cm and a weight of 5.6 kg, was collected in March 2000, a short distance upstream from Myinthar-Kyarnyut Village at Khayansat Kone village (23°16.30'N; 95°58.99'E), a two day boat ride north of Mandalay (21°58.75'N; 96°03.50'E) on the Ayeyarwaddy (=Irrawaddy) River (Fig. 3B). The species is said to be locally rare, since fishermen at the village of capture report encountering only about one per year. Other fishermen at Letpangon Village (23°20.16'N; 96°00.55'E) were also familiar with the species but again considered it to be rare.

Thailand.- The first vouchered report of *Chitra* from Thailand probably reflected the specimen (MNHN 8003) received by Bocourt during his 1861-62 sojourn (Bourret, 1939), but upon recent examination by Roger Bour (pers. comm.), this specimen proved to be a misidentified *Pelochelys cantorii*. Later, Smith (1931) documented three Thai *Chitra* specimens, all of which he deposited in the British Museum of Natural History. They were reportedly caught in the upper reaches of the Ratburi River [= Kanchanaburi River; = Mae Klong River, see Thirakhupt and van Dijk, 1994: 210], "where the waters are clear and the banks sandy." In the BMNH catalogue, specimens donated by M. A. Smith include BMNH 1921.4.1.197, identified as "head, limbs, tail in spirit," from Ban Pong, C. Siam; BMNH 1926.12.16.1, a skeleton from the "Ratburi" River, Kanburi, Siam; and BMNH 1931.11.2.1, which is just a humeral gland and duct in spirit. Later, an additional specimen (BMNH 1974.24.5.1), a shell and skeleton also from Ban Pong, were received from the M. A. Smith Collection.

Cox et al. (1998) reported that, in Thailand, the species occurs in the Mae Klong river system, and Thirakhupt and van Dijk (1994), agreeing here with Cox added records for the Srinagarind Reservoir, Kanburi (presently Kanchanaburi) Province (CUMZ

(R)1991.08.23.1), and for three specimens captive-hatched from the Khwae Noi River, Kanburi Province (CUMZ (R), unnumbered). The Srinagarind record was based upon an enormous softshell accidentally entangled in a submerged mesh upstream from the hydroelectric dam in 1989 (Amonratanasareegul, pers. comm. to P. P. van Dijk, 1992). Kitimasak and Thirakhupt (2002) discuss new records of *Chitra chitra* specimens found in the Mae Ping River of the Chao Phraya river system of Thailand. With specimens from the Mae Klong and Mae Ping Rivers, a *Chitra chitra* research and breeding program has been run for nine years by the Inland Fisheries Development Center in Kanchanaburi. The goal is to save the species from overcollection, pollution and the detrimental effects of reservoir dams on nesting areas.

There are also three Thai specimens, without detailed collecting data, in the Harvard collection (MCZ 29486-88). Published photographs of Thai specimens include those in Advanced Thailand Geographic Magazine Vol. 36 (July-August, 1999; foldout between pp. 81-87); Lim and Das (1999); Nutaphand (1979, 1986, 1990); Techacharoensukchera (1991); Thirakhupt and van Dijk (1994, two separate individuals); Cox et al. (1998); and Fritz and Obst (1999). Available distribution maps (e.g., Nutaphand, 1990; Iverson, 1992) seem to agree that the distribution in Thailand is extremely restricted (see Fig. 3C).

Malaysia.- Well over a century ago, Günther (1864) reported that *C. indica* "is frequent in the estuaries of the Malayan Peninsula." He also published an illustration (Plate VI. fig. c.) labeled "*C. indica*" (see neck "V" and *Chitra* head pattern) that Smith (1931) declared "represents a *P. bibroni* [referring to what is currently *P. cantorii*], but with the markings of a *Chitra indica*". We concur with Smith, supported by Gray (1864:90), who stated that Günther's "*Chitra indica*" is "not Gray" [meaning here, not *C. indica* (Gray 1831a:18)], and who also states Günther studied ("soaked") Cantor's (1847) specimen (now known to be *Pelochelys*, see Appendix), and "says he [Günther] observed" a *Chitra* pattern. Günther was therefore erroneously trying to illustrate a *Chitra* pattern for Cantor's specimen

(see Gray, 1870:91), not knowing the sympatric genus *Pelochelys* existed. Günther (1864) added that Mr. Cuming had brought home some “fine examples” (of *Chitra*), said to have been procured in the Philippine Islands. (Gray, 1855), also mentioned the same Philippine specimens. Almost certainly these Philippine records pertain to *Pelochelys cantorii* rather than to *Chitra* (see *P. cummingii* in Appendix), further demonstrating the confusion at that time between the two genera.

Smith (1922) commented (about *Chitra*): “The discovery of this species, one of the largest of the freshwater turtles, in the Malay Peninsula is a fine extension of its known range. It has previously been recorded from the Ganges and Irrawady river systems. This turtle has also been met with in the Ratburi River, western Siam, two adult specimens having been caught near Kanburi. These two examples, which I examined alive, differed from the description of the Indian form in that the disk was marked with numerous, pale broad lines and angular markings”. Smith (1930) tells of a *Chitra* specimen from the Tahan River, Pahang, Malaysia (Fig. 3C). Smith (1931) remarked further that Robinson and Kloss obtained a specimen at the foot of Gunong Tahan, in the Malay Peninsula.

Lim and Das (1999) included *Chitra* (a composite account of *C. indica* and *C. chitra*) in their book entitled “Turtles of Borneo and Peninsular Malaysia,” and observed that the first West (i.e., mainland) Malaysian specimen was the one caught in Kuala Tahan River, Pahang, in 1922 and cited as obtained by “F. M. S. Museums” by Smith (1930); they commented that there were no recent records. Sharma and Tisen (2000) listed *C. chitra* in the Malaysian fauna, but observed that its current distribution was unknown, the historical records being from Taman Negara. Research and interviews conducted by them along several rivers over the last few years yielded neither specimens nor anecdotal information. They concluded that the species may have been hunted out well before any populations could be verified.

E. O. Moll, an expert on Malaysian freshwater turtles (e.g., Moll, 1980; 1984; 1989), com-

mented (in litt. to P. P. van Dijk): “There is an old record by Smith for the Pahang River and I think I saw one surface in a tributary of that river near the National Park (it could have been a *Pelochelys*). It is the only *Chitra* that I ever saw in Malaysia. They are extremely rare. One of [John M.] Legler’s other students bought one in a Chinese shop in Kuala Lumpur but it had no data.”

A commercial videotape entitled “Shocking Asia” (Magnum Entertainment, Los Angeles, USA, 1986) includes a sequence showing the capture and butchering of an adult *Chitra* specimen, ostensibly in Malaysia. The dorsal pattern of the specimen, which is very large (ca. 100 cm), includes the markings characteristic of full-size eastern *Chitra* (i.e., bold, imperfectly symmetrical pale yellow streaks without fine structure, and “zig-zag” nuchal markings, on a dark background), and, while the exact locality is unavailable, there is no obvious reason to doubt that the event occurred in Malaysia. Recently, Mr. Keng Liang (Anson) Wong, of Penang, Malaysia, received several live specimens that had been caught “20 miles northeast” of Kota Tinggi, Johor State, southern peninsular Malaysia (Fig. 3C). Mr. Wong also reports knowledge of *Chitra* found in Terengganu State, eastern peninsular Malaysia.

Indonesia.- Probably the first report of Recent *Chitra* from Indonesia was in a generally overlooked paper by Müller (1923). In translation, the section pertaining to *Chitra* reads: “In the year 1908, Dr. Elbert presented to the Bavarian State Museum a series of reptiles consisting for the most part of skeletons of monitors (*Varanus*), crocodiles and turtles. There was only one container with alcoholic specimens, with a collective label indicating that the specimens were from Java, or some possibly from Sumatra. Among the skeletons there was also *C. indica* (Gray, 1831) with the attached tag indicating “Buitenzorg, Java” (now Bogor, Jawa Barat). The species has not previously been reported from the Indo-Australian archipelago. A confirmation of this striking locality record through the procurement of further specimens is therefore of interest.”

Two skulls of Indonesian *Chitra* are available in European museums: NMW 162 (“N. Küste

Sumatra”) and RMNH 7054 (“Java”). Webb (1995) cast doubt upon these recorded localities, but we consider them to be credible. Samedi and Iskandar (2000) reported *C. chitra* to be “rare” in both Sumatra and Java, and Iskandar (2000) gave the Indonesian vernacular name for the species as “labi-labi bintang”. His statement of range included southern Thailand, Malaysia, several localities in Sumatra (Aceh, Sumatra Utara, Riau, Jambi), and Java (Karimun Jawa Islands, Ciliwung, Bengawan Solo). In fact, although the presence of this enormous freshwater turtle species in Java is little recognized in the western world, it is already protected by law (as *C. indica*) in Indonesia, (Government Regulation Act. No. 7 and 8 of 1999; Samedi and Iskandar, 2000) based upon the presumed rarity of the species because it has been known from so few specimens. These same authors cite *Chitra* (as *C. indica*) from Karang Gading Wildlife Reserve, South Sumatra; Barbak National Park, Sumatra; and the delta of the Banyuasin-Musi rivers, South Sumatra, as well as Lake Sentarum Wildlife Reserve, West Kalimantan [Borneo], although by the authors’ own admission some of these records are questionable, and the possibility exists that some of these reports involved misidentified *Pelochelys*. On habitat likelihood alone (it being observed that *Chitra* requires large, lowland tropical rivers), the Karimun Jawa locality (a group of small, rocky islands between Java and Borneo) is probably in error, even though there is a large specimen in the CRI collection, collected by locals for F. Yuwono, ostensibly from there.

Shepherd (2000) was advised by a major turtle exporter in Medan, Sumatra, that specimens of *C. chitra* were occasionally brought in to his company from various Sumatran localities (excluding the Tembilahan area, where *Amyda* is the only trionychid found). Recently, we have confirmed the presence of *Chitra* on the island of Java, and specimens of *Chitra* said to be from “Lampung”, eastern Sumatra have also been obtained (see below, also Fig. 3D).

FIELD NOTES

In Java, most turtles were caught by professional collectors in a tidal creek of the Pasuruan River, near Pasuruan, Probolinggo District, East Java (Fig. 3D). This creek, about 15 m wide and 1-1.5 m deep, had a uniform temperature of 26 C when measured at several points in late July 1997. The location, taken by Global Positioning Satellite System (GPS), was 7°39.83’ S and 112°57.30’ E. Most of the area was utilized for low-intensity agriculture, with some dense vegetation around the creek itself, and scattered homesteads.

A smaller number of turtles were caught in the Solo River (the largest river in Java, Fig. 3D) at a point in East Java Province about 10 km west of the provincial border with Central Java (7°09.87’ S; 111°38.56’ E). At this point the river was wide (at least 100 m), but the season was dry and water levels were low, with extensive sandbanks exposed and water levels shallow (less than 1 m). The area was quite densely populated, with villages just beyond the seasonal sandbanks, much trash in evidence, and numerous locals (especially children) greatly interested in our activities. A local team of turtle hunters was recruited, and, utilizing the “poking” (see below) technique, was able to catch a small *Chitra* (CL 17.8 cm, CW 18.1 cm) within 15 minutes. Later a larger specimen was caught at the same site, and we were given two others. The capture team indicated that, in their experience, *Chitra* was the only trionychid present at this site; there was no evidence of *Amyda*, *Pelochelys* or *Dogania*.

The actual capture technique used in Java, carried out by local professional turtle hunters under observation by PCHP and F. Yuwono, was for four hunters to walk in water of appropriate depth for wading (up to about 120 cm, sometimes more), constantly poking the bottom substrate with spears fabricated from green bamboo poles, about 2-3 meters long and ca. 4 cm thick, each with a very sharp barbless iron point rigidly attached. The overall objective was to pin down a concealed turtle by perforating it through the leathery carapace flap, and then to bring it to the

surface. Smaller turtles are handled by first locating the head, then picking them up by the sides of the carapace with both hands. Others may be enmeshed in a net and brought ashore. Large turtles may be immobilized by impaling the carapace flap in this way by each of two or even more members of the team. One very large adult *Chitra* in the Pasuruan River west of Probolinggo was pinned down by four hunters, but succeeded in swimming with all four in tow for about 100 meters, then turning around and returning upstream, before breaking or extracting all four spears and escaping. Both *Chitra* and *Amyda* are caught in this way; we were advised that *Chitra* are usually lightly buried under a shallow deposit of silt, whereas *Amyda* are generally found deeper.

Another technique employed by some commercial softshell hunters in East Java utilizes a high-ampère battery pack that can be worn as a backpack, attached to two long, pointed electrode shafts with insulated handles. When these electrodes both make contact with a submerged turtle, it is stunned by the electric shock and can be caught by hand.

Interview data with Saiful Anwar in the Pasuruan area indicated that *Chitra* was found in the eastern part of Java, localities personally known to him including Lejoso (between Pasuruan and Lekok), Lumajang (south of Bromo), and Jember (south of Kukusan). *Chitra* was generally sympatric with *Amyda cartilaginea*, and when a turtle was located in the bottom substrate, it was not certain which species it was until it was brought ashore, apart from the fact that *Chitra* reaches a larger size than *Amyda* – weight up to 150 kg. In general, *Amyda* was more abundant than *Chitra*, but both were becoming scarce. The informant had caught softshells for thirty years, but was unfamiliar with *Pelochelys*. He indicated that both sexes of *Amyda* reached a similar size, but that *Chitra*, which he sold alive, could not easily be sexed externally. Both species would sometimes bask on mud flats in the early morning (0600-0900 h.) with legs extended, but would quickly return to the water when disturbed. Low tide during the dry season was the best time to catch them; the

entire section of the Pasuruan River occupied by *Chitra* (i.e., downstream from the bridge) was strongly tidal.

MATERIALS AND METHODS

Nearly two centuries since the first description, there is still very scant information on geographic variation or speciation within the genus *Chitra*. Even Nutaphand's definition of the second species (*C. chitra*) rests almost solely upon minor comments by Smith (1930). This dilatory scientific advancement stems from several causes, as follows:

Adult turtles of the genus *Chitra* are large and highly sought after as food. They spend most of their time concealed in benthic substrates in large rivers, which makes them inaccessible. By the time the turtles reach scientists they are rarely alive. Most museum specimens are either lacking collection data or with only a general indication of provenance. Most collections only include single range-state specimens making comparisons of species from different range-states difficult. The gross distinguishing features of *Chitra* are skin and shell patterns, yet these characters easily deteriorate upon death. These patterns are subject to marked variation even within a population, and vary with ontogeny. Over-exploitation and habitat destruction have made *Chitra* rare in almost all parts of their range. *Chitra* are difficult to keep alive, both in transit and in captivity.

Our methodology was to compare the phenotypic, morphological, zoogeographic and phylogenetic data obtained from the study of literature, published colour illustrations, and both preserved and live specimens of *Chitra* available to us. Current published live inventories identify only the San Diego and St. Louis Zoos (USA) as each having a pair of live *Chitra*, with two adults and several juveniles in the Khao Kheow Zoo in southern Thailand, and the breeding group mentioned above in Kanchanaburi, Thailand. The Madras Crocodile Bank (Vadanemmeli, Tamil Nadu, India) also has live *Chitra* from time to time. One of the authors (WPM) has series of live subadult animals from Bangladesh, Java, Sumatra, Malaysia, Thailand, Pakistan, and Myanmar, upon which the descriptions below are based.

Chitra indica, the generotype, is considered to be the “baseline” taxon with which other populations were compared.

We were able to accumulate adequate live samples of *C. indica* from Bangladesh (n= 7) and Pakistan (n= 5). Live Myanmar *Chitra* specimens (n= 8) were obtained from the market in Ruili, Yunnan, along with three preserved Myanmar specimens and a skeleton in the CRI collection (PCHP 4896, 4897, 5050, 7059), plus we saw the coloured photograph in Platt (2001). We also studied a series (n = 18) of Java *Chitra* examined and photographed alive at the time of capture and while in the WPM collection, most since liquid-preserved or prepared as skeletons (PCHP 4629, 4936, 4937, 4965, 4897, 4975, 4988, 4995, 5001, 5002, 5003, 5049, 5052, 5053 and MZB 264, 265, 266, 267), captured for us by supervised professional turtle hunters. While we did not personally supervise the capture of the first two groups, we have confidence that they were local in origin, and we ensured by visual inspection (and later genetic characterization) that they were essentially homogeneous and showed the overall features that we came to recognize in each geographically isolated population. Our series of specimens from Thailand (i.e., topotypic *Chitra chitra*) consisted of a few living Thai specimens seen in collections in Thailand, two living specimens in the collection of WPM, and a skeleton in the PCHP collection (n= 6), and for comparison we had access to an inventory of published illustrations of specimens, nearly all in colour (see references above). We have live specimens from Malaysia (n= 4), that are clearly of the overall *C. chitra* phenotypic “group” (see below).

The following museum acronyms are used herein: AMNH = American Museum of Natural History, New York; AMS = Australian Museum of Science, Sydney; BMNH = British Museum (Natural History), London (officially, but not preferably cited as NHM = The Natural History Museum, London; Colin McCarthy, pers. com.); CRI = Chelonian Research Institute, Oviedo, Florida (houses PCHP = Peter C. H. Pritchard collection); KP(CUMZ(R)) = Chulalongkorn University Museum of Zoology (Reptile), Thai-

land; MCZ = Museum of Comparative Zoology, Harvard University, Massachusetts; MZB = Museum Zoologicum Bogoriense (Cibinong); MNHN = Muséum National d’Histoire Naturelle, Paris; NMW = Naturhistorisches Museum Wien (Austria); RCS = Royal College of Surgeons (London); RMNH = Rijksmuseum van Natuurlijke Historie, Leiden; ZISP (formerly ZIL) = Zoological Institute, Sankt-Petersburg; ZSI = Zoological Survey of India, Calcutta.

Carapace length (CL) of live and alcohol preserved specimens is herein the straight midline distance from the anterior bony carapace (disc) to the posterior edge of the leathery carapace.

Carapace length (CL) of skeletal specimens is herein the curved midline distance from the anterior bony carapace (disc) to the posterior bony carapace.

Carapace width (CW) of skeletal specimens is herein the curved distance between the widest points of the bony carapace (excluding rib tips).

CHITRA: GENERIC DESCRIPTION

The following combination of characters distinguish *Chitra* from all other genera of softshell turtles: Trionychid turtles characterized by gigantic adult size; a wide flat dorsal disc subject to little if any ontogenetic change in relative size or shape of either the leathery shell or the bony disc; four plastral callosities that form very early in life, and retain their shape throughout ontogeny; a very specialized head form with extreme anterior displacement of the orbits, overall narrowing, and marked elongation; absence of cutaneous femoral valves under which the hind limbs retract; a unique head, neck and carapacial pattern; and a unique combination of skeletal features (see below).

The forelimbs of *Chitra* bear both sharp-edged anterior scales or lamellae, and elongate, round-edged structures along the distal and lateral aspect of the forelimbs that serve to support and deploy the digital webbing to maximum advantage, for which we use the name “pseudodigits” (Fig. 4). The numbers of these structures are quite variable, and for this reason they were examined and recorded in specimens of each of the populations studied. The samples



FIGURE 4: Illustration of forelimb lamellae and “pseudodigits” of *Chitra indica*.

are too small to merit detailed statistical analysis (Table 1), but it would appear that, in the *C. indica* and Myanmar samples, the lamellae usually number 3 or 4, and in the *C. chitra* samples (Thai, Malaysian and Indonesian) the mean number is 2. The pseudodigits do not appear to show significant geographic differences.

Skeletal features of turtles of the genus *Chitra* may be characterized as follows:

Head: The skull is extraordinarily elongate, streamlined, anteriorly depressed, and narrowed, the widest point being at the lower margin of the quadrate bones, between the tympanic cavity and the jaw articulation (Fig. 5). As an adaptation to accommodation of the extremely long mandible and wide gape, and the associated elongated retractor mandibulae musculature, the supraoccipital process is not only deep (except towards the posterior tip) but very long, and the

squamosal bones also show remarkable posterior development. Nasal septal ridges are absent (present in *Pelochelys*). The orbits show extreme anterior displacement, and this is accompanied by a remarkable posterior elongation of the frontals and anterior elongation of the parietals. The vomer-prefrontal struts are absent (present in *Pelochelys*). The postorbital “bar,” actually an extensive postorbital area, has a minimum width that is slightly more than twice the horizontal width of the orbit (postorbital bar and orbital diameters about the same in *Pelochelys*). The single premaxilla, although probably always present, is reduced to a minuscule triangular element, dorsal to which the maxillae make contact at the base of the apertura narium. The intermaxillary foramen is almost or completely absent (relatively large in *Pelochelys*). The prootic bone makes up virtually the entire

trochlear surface for the sliding movement and redirection of the jaw musculature. The triturating surface has a distinct sharp-edged continuous ridge posteriorly (absent in *Pelochelys*). The inner surface of the dentary has a distinct lingual ridge forming a horizontal shelf, prominent throughout its length except around the mandibular symphysis (absent in *Pelochelys*).

The hyoid structure of *Chitra* is enormous. In fully mature specimens, the corpus hyoideus includes eight ossifications; in younger specimens there are six. The anterior hyoid horns (cornua branchiales I) are each composed of a single ossification, while each posterior horn is composed of an elongate basal bony element sutured to a short middle component which in turn sutures with a wide, curved posterior element. Such a

configuration is shared with *Pelochelys*, but is otherwise unique.

Cervical vertebrae: The eight cervical vertebrae, with the exception of the atlas (a composite of four unfused bones), are all highly elongate, and bear no ventral processes. A dorsal process, for insertion of the musculature that propels the powerful forward thrust of the neck, is present on each of elements IV to VII, the most elevated by far being on cervical VI. Ginglymoidy is present on the articulations of cervicals V-VIII, and the posterior joints of cervicals III and IV are also broadened although not actually doubled.

Carapace: The bony carapace (disc) is very flat and about as wide as long, with an antero-posteriorly foreshortened nuchal bone, and usually eight discrete neural elements, the first four hexagonal with short sides posteriorly,

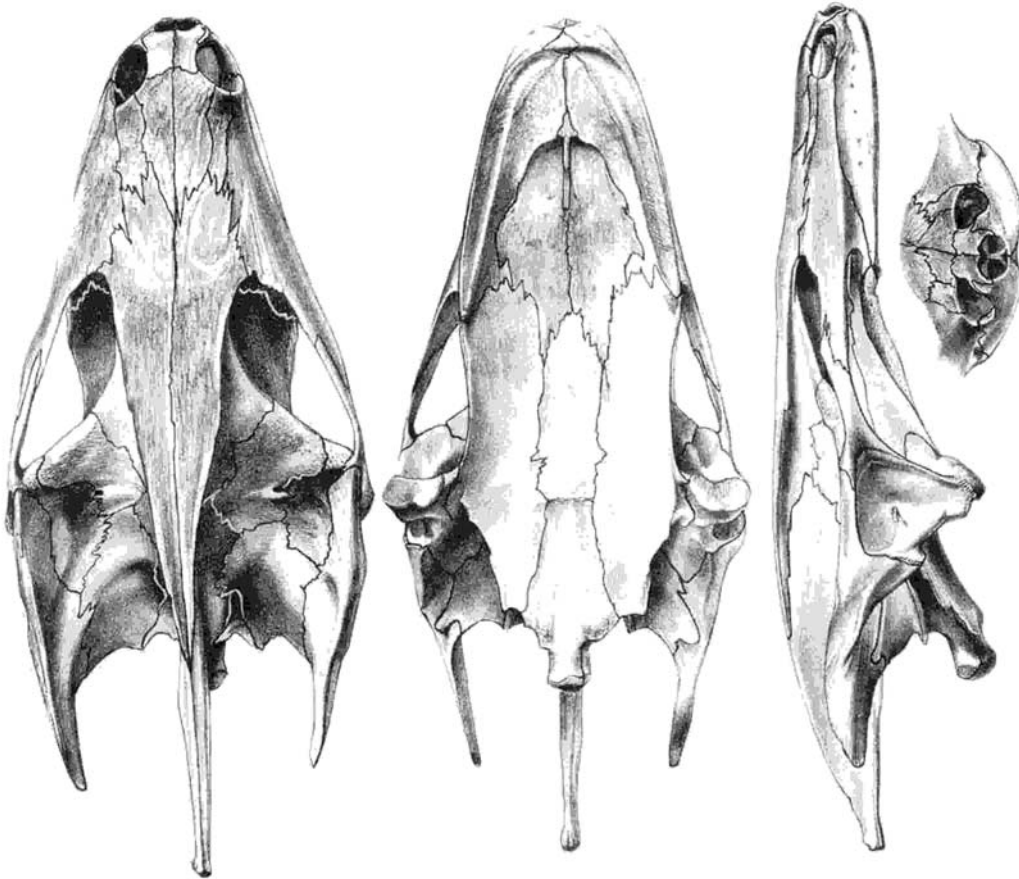


FIGURE 5: *Chitra* skull illustrations (taken from Gray 1855).

the fifth rectangular, the sixth and seventh hexagonal with short sides anteriorly, and the eighth pentagonal. The first neural element may correspond to neurals I and II (fused) of certain other turtles, including *Aspideretes* and the cyclanorbines (see Meylan, 1987). Occasional variant configurations occur, including asymmetrical realignment of the suture between neurals V and VI, rendering both of these elements pentagonal. The eighth pleurals are wide and well developed, and contact each other along the midline throughout most of their length. The exposed rib-tips are short and stout, and protrude beyond the bony carapace throughout life; the eighth ribs show none of the posterolateral elongation and flexibility typical of many trionychids. The costal bones are fully developed throughout life, and intercostal fontanelles are absent. The costiform processes of the nuchal bone are expanded and grooved, and they curve posterolaterally, often overlapping the first pleural bones. The entire surface of the bony carapace is coarsely cratered and pitted, the concavities sometimes forming vaguely linear or vermiform configurations. The posterior margin of the bony carapace is distinctly and broadly incurved throughout life.

Plastron: The plastron consists of nine bones. The anterior processes of the epiplastra are relatively short, and sinuous in vertical profile. The entoplastron is very large and boomerang-shaped, the slender blades meeting at an angle of approximately 80-85 degrees. Callosities are absent on both entoplastron and epiplastra. On each side, the hyoplastron and hypoplastron are connected by a suture that laterally runs perpendicularly to the midline of the plastron, but towards the midline this suture angles sharply anteriorly. Each hyo-hypoplastral unit is almost completely covered by a superficial callosity that is fully developed even in young specimens. Each xiphiplastron also bears a single callosity that covers almost its entire surface. Along the anterior part of the mesial edge, the xiphiplastra show coarse, angular interdigitation (allowing extensive kinesis), while posteriorly the two bones enclose a permanent fontanelle. The anterior border of each xiphiplastron bears a lateral

spur that, together with its smaller neighbor, embraces a corresponding angular spur in the posterior of the hypoplastron, and toward the midline smaller spurs of decreasing size may be present. Permanent entoplastral and mid-plastral fontanelles are present, the former penetrated to some extent by a series of sharp prongs adorning the rounded anteromedial face of each hypoplastron. Each hypoplastron bears an array of stubby protuberances on its posteromesial edge, that juxtapose but do not interdigitate with those of the opposing hypoplastron. There is frequent asymmetry between corresponding plastral elements in terms of the number of spurs, notches, or interdigitations that are present. Anterolaterally each hypoplastron is extended into a bifurcate prong, and the posterolateral corner of each hypoplastron bears two or three prongs. These prongs extend well beyond the lateral limits of the bony carapace.

Limb girdles: The pelvis is very broad and flaring, has a very large, undivided puboischiatic fontanelle (= thyroid fenestra of Romer, 1956 and Meylan, 1987), extremely well-developed pectineal processes, and strong metischial processes. The pectoral girdles are typically trionychid, the acromion process of the scapula, the main body of the scapula, and the coracoid radiating in three directions from the glenoid fossa, with the coracoid both the longest and the broadest of the three.

Extremities: The humerus and femur are of very similar length and appearance (although the open entepicondylar groove always distinguishes the former), but the tibia and fibula and the phalanges of the posterior limbs are considerably longer than the corresponding elements of the forelimbs. Each limb bears only three claws (on digits 1-3), and on both fore- and hind limbs the five digits show progressive reduction in robustness from the first to the fifth. Digit 4 of the forelimb may show remarkable elongation and hyperphalangy, with as many as six phalanges.

Skeletal differences between the various populations and taxa of *Chitra* have not been fully documented. Carapacial proportions show some ontogenetic change, but a comparison between Indian (Hindon River) and Burmese

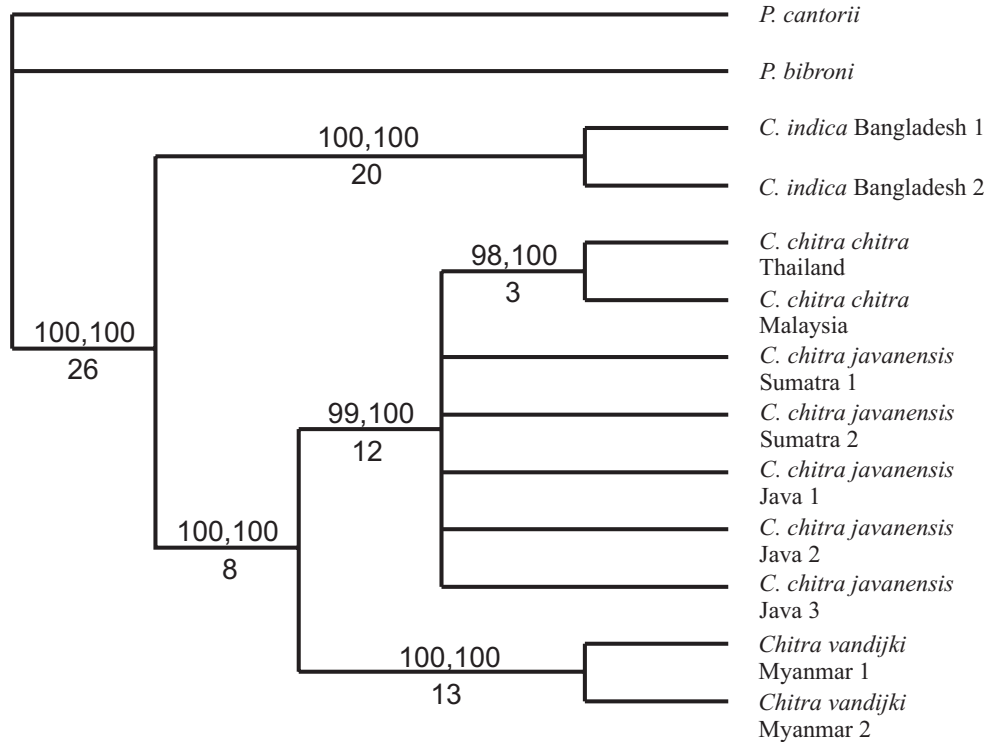


FIGURE 6: Bootstrap consensus phylogeny depicting the relationships within the genus *Chitra* based on likelihood and parsimony analysis (both indicate identical relationships) of the ND4 gene. Numbers above the node represent the bootstrap support for the node in 1000 replicates under likelihood on the left, and under parsimony on the right. Numbers below the node indicate decay index for the node. Redrawn from Engstrom et al. (2002).

(Ayeyarwaddy River) bony shells of virtually identical length is interesting. The Indian shell (CL 36.1 cm; CW 32.7 cm) was narrower than the Myanmar one (CL 36.0 cm; CW 36.8 cm), and had distinctly narrower neural bones. Taking neural I as exemplary, in the Indian specimen the width/length ratio of this bone was 70.6%; in the Burmese one it was 84.2%; and in three Javanese specimens of slightly larger size it was 78.2, 80.2 and 82.8%. The Indian specimens examined also generally had smaller, narrower, and more tapering exposed rib ends, and the edge of the bony carapace was progressively thinned, whereas in the Burmese and Javanese specimens the edge of the bony carapace was thick, and terminated abruptly rather than gradually. In overall contours, the bony carapace of half-grown Javanese specimens was more convex than those of specimens from Myanmar, and there was a tendency toward a slightly bilobed configuration, with a depressed vertebral region, in the former.

SYSTEMATICS

In striking contrast to its relative *Pelochelys*, which is regularly encountered in estuarine or even marine environments, the ability of *Chitra* to cross oceanic barriers remains undemonstrated. Furthermore, the consistent external differences in *Chitra* (primarily in markings and colour) between the populations in separate mainland river basins (i.e., the Indus/ Ganga/ Brahmaputra systems of Pakistan, India and Bangladesh; the Ayeyarwaddy system of Myanmar; and the Mae Klong system of Thailand) strongly suggest that genetic isolation is essentially complete. We still lack many details of the distribution in the insular part of the range (Indonesia) as well as on the Malaysian Peninsula. Nevertheless, the ability of the genus to have colonized rivers as far east as central and eastern Java (today separated from the continent of Asia by two marine barriers, the Straits of Malacca and Selat Sunda) may be explained in

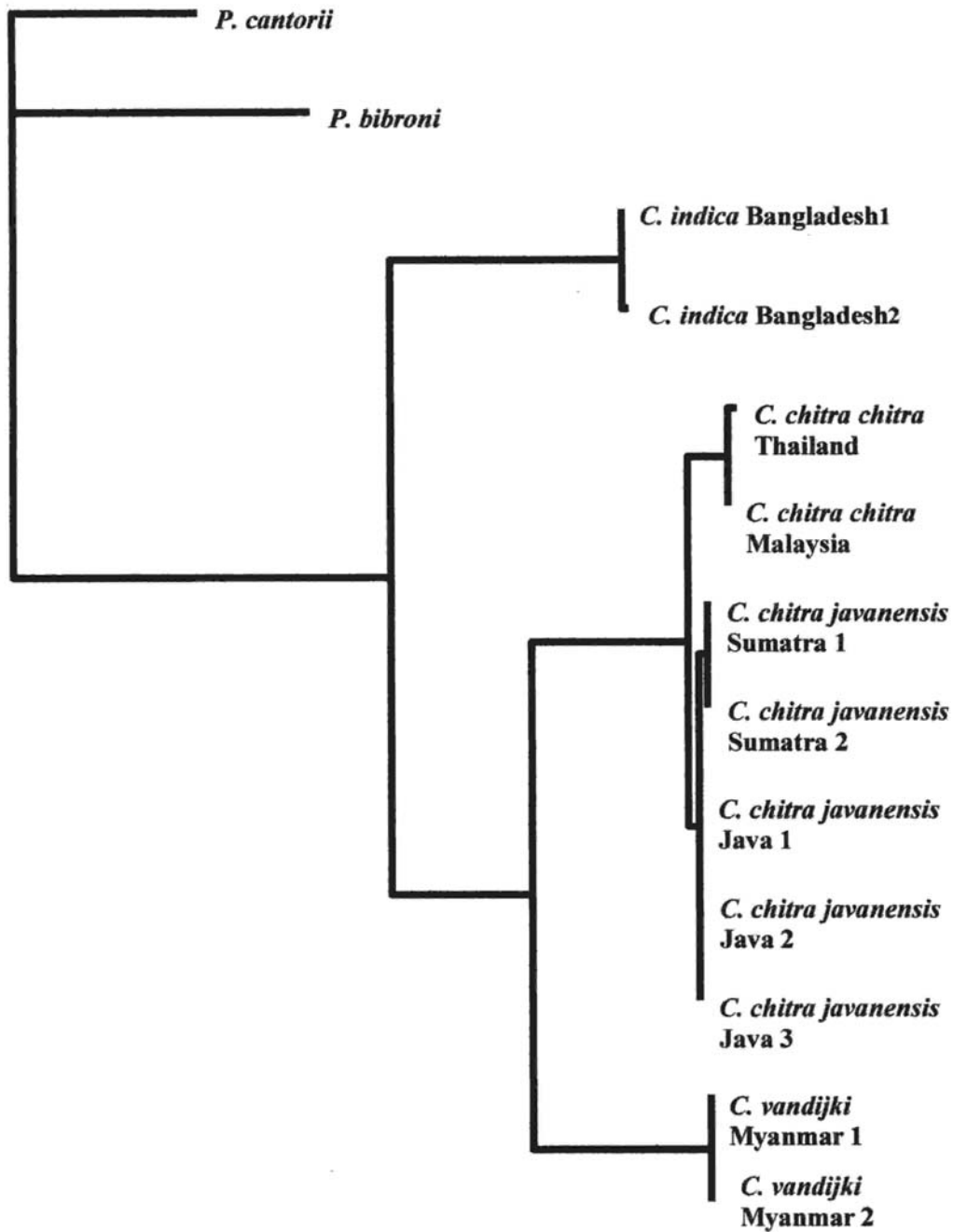


FIGURE 7: The single most likely topology of the phylogenetic relationships within the genus *Chitra* based on likelihood analysis of the ND4 gene. This topology shows the monophyly of the island and mainland clades within *Chitra chitra*. Redrawn from Engstrom et al. (2002).



FIGURE 8: Narrow-headed softshells of the genus *Chitra*: (A) *C. indica* (Dacca market, Bangladesh); (B) *C. vandijki* (Ruili market, Yunnan, China); (C) *C. chitra* (vicinity Kota Tinggi, Johor, Malaysia); (D) *C. c. javanensis* (Pasuruan River, Java, Indonesia).

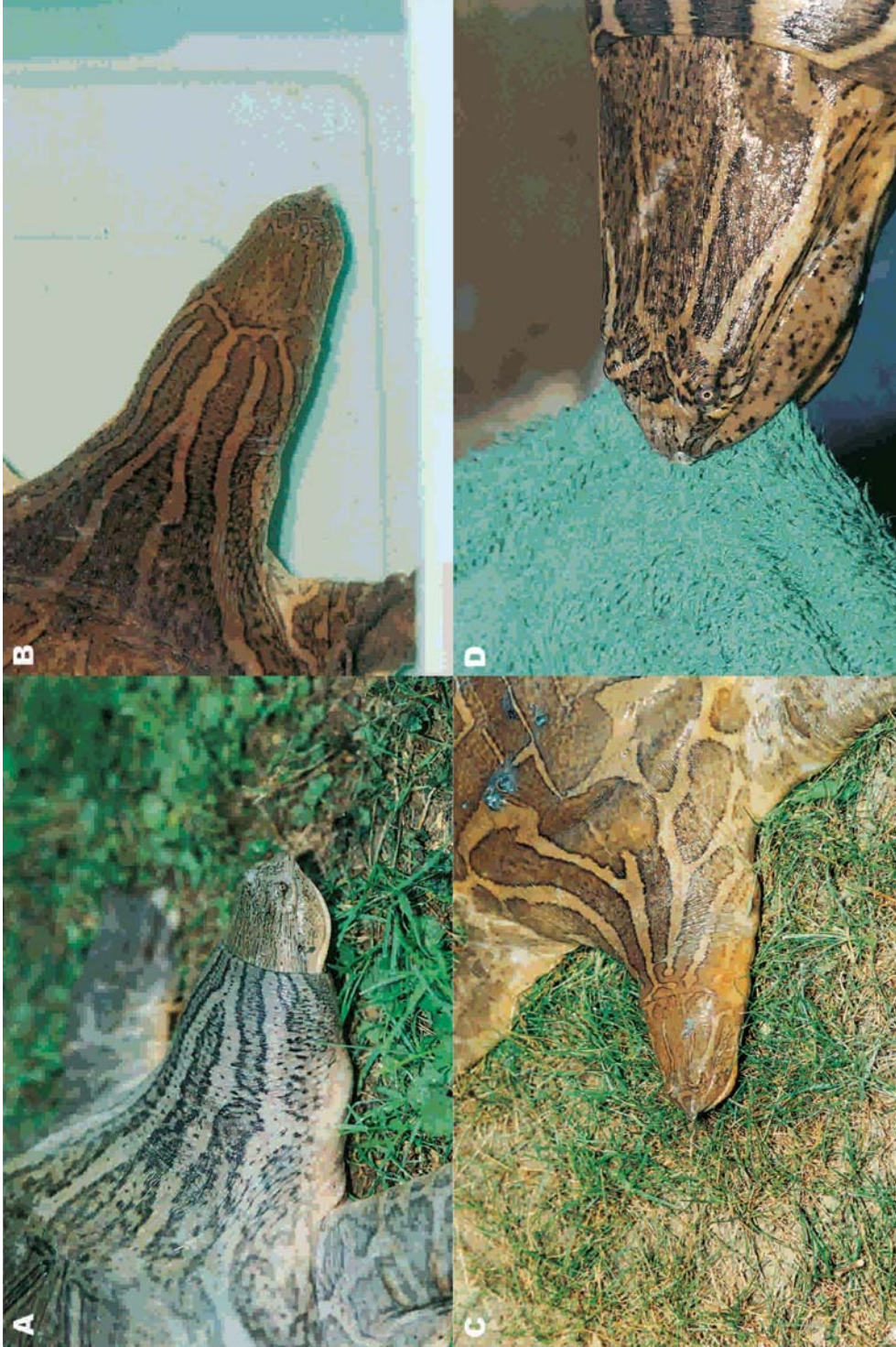


FIGURE 9: Head markings of softshell turtles of the genus *Chitra* (same locality data as Fig. 8): (A) *C. indica*; (B) *C. vandijki*; (C) *C. c. chitra*; (D) *C. c. javanensis*.

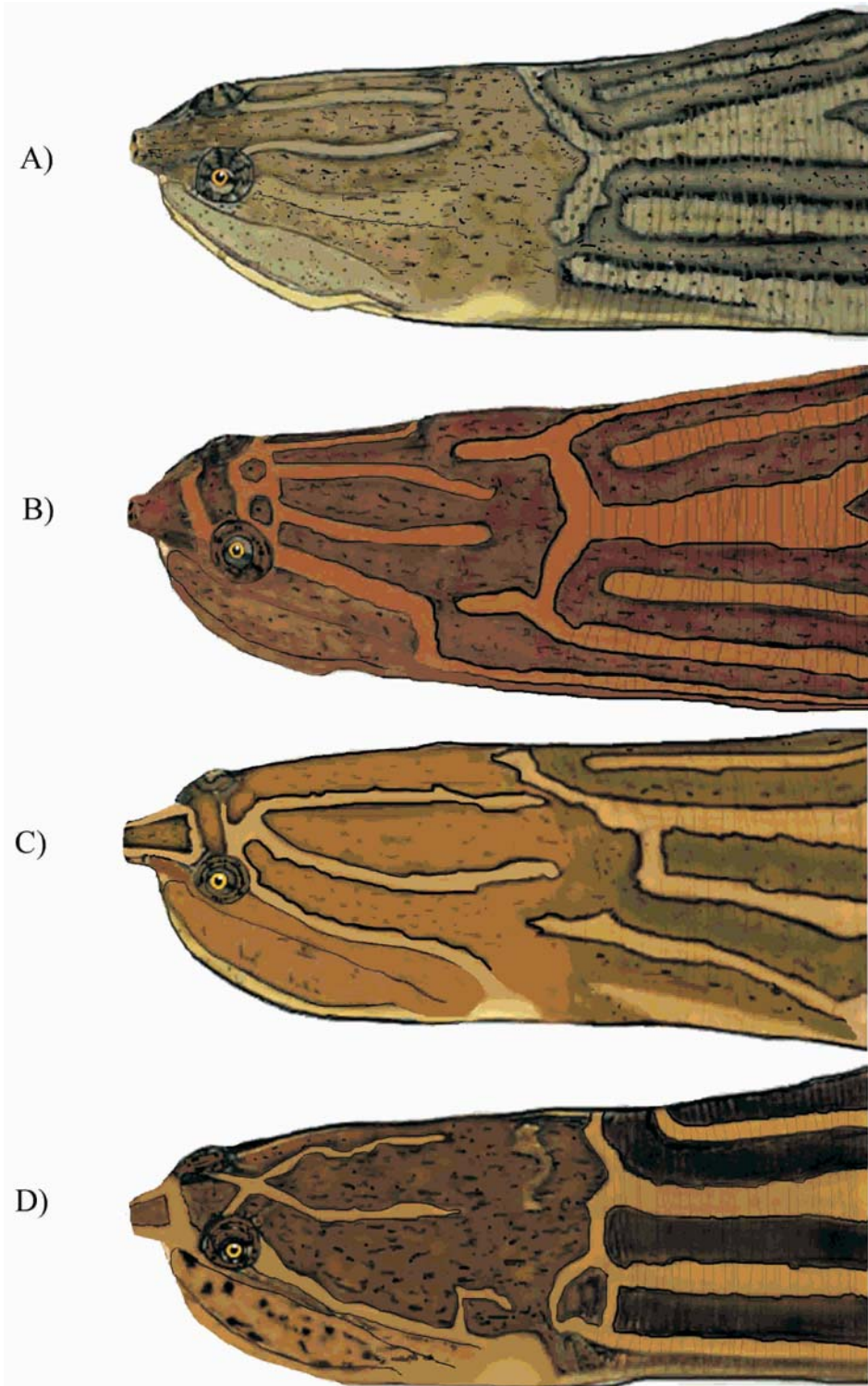


FIGURE 10: Original watercolour illustrations of *Chitra* head and neck patterns. (A) *C. indica*; (B) *C. vandijki*; (C) *C. c. chitra*; (D) *C. c. javanensis*.



FIGURE 11: Holotype of *Chitra vandijki*.



FIGURE 12: Holotype of *Chitra chitra javanensis*.

TABLE 1: Numbers of forelimb lamellae and pseudodigits in several *Chitra* populations.

Specimen	Left lamellae	Right lamellae	Left pseudodigits	Right pseudodigits
<i>Chitra indica</i> (Bangladesh)				
1	2	4	2	2
2	3	4	4	3
3	3	4	2	2
4	3	3	2	2
5	4	4	4	4
6	3	3	2	2
7	4	4	0	0
<i>Chitra vandijki</i>				
1	3	3	1	1
2	4	3	2	2
3	2	2	2	2
4	2	2	2	2
5	3	2	2	3
6	3	3	1	1
7	3	3	2	2
8	3	3	2	2
<i>Chitra chitra</i> (Thai, Malaysian, Indonesian)				
1	2	2	2	2
2	2	2	2	2
3	2	2	1	1
4	1	3	2	2
5	2	2	2	2
6	3	2	2	2

part by the extremely narrow nature of both of these straits, and in part by the fact that, during Quaternary times when sea levels were lower, the entire range of the genus *Chitra* was connected by land bridges

In parallel with our phenotypic, morphological and zoogeographic studies Engstrom and colleagues have conducted molecular studies of the same *Chitra* populations. Engstrom et al. (2002) found three very well supported deeply divergent evolutionary lineages within the genus *Chitra* (Figs. 6 & 7). These lineages correspond with the three species recognized here: *Chitra indica* (Gray, 1831a), *Chitra chitra* Nutaphand, 1990, and *Chitra* sp. nov. from Myanmar, described herein. The high level of molecular divergence (Table 2, 8.6%) between *Chitra indica* and the clade containing the *C. chitra* complex and the Myanmar *Chitra* sp. nov. is comparable to divergence levels between other well-recog-

nized species in the family Trionychidae (Weisrock and Janzen, 2000; Engstrom et al., unpublished data) and indicates that these two lineages have a very long history of independent evolution. Similarly the sequence divergence of 5.1%-5.3% between the Myanmar *Chitra* and members of the *C. chitra* complex (Table 2) is higher than comparisons within North American trionychid species (Weisrock and Janzen, 2000) and indicates that these two lineages have also shared a long history of independent evolution. Based on this clear phylogenetic pattern, Engstrom et al. (2002) supports the recognition of three species within the genus *Chitra*.

Engstrom et al. (2002) also observed low levels of geographically structured molecular variation within the *Chitra chitra* complex that are consistent with the subspecies designations presented herein. The two mainland *Chitra chitra* samples differed from each other by a single base pair transition. All seven individuals from Java, of which three were reported by Engstrom et al. (2002), plus four by Engstrom and McCord (2002) had identical DNA sequences. These Java animals differed by a single base pair transition from the two identical sequences from Sumatran specimens. These two island populations differed by 1% from mainland populations. This level of sequence divergence is similar to the level of divergence observed among subspecies of North American softshelled turtles (Weisrock and Janzen, 2000).

In contrast there is almost no molecular variation within *Chitra indica*. The two individuals from Bangladesh sequenced by Engstrom et al. (2002) differed from each other by a single transition. Engstrom and McCord (this volume) have extended this sampling to include another individual from Bangladesh as well as two individuals from Pakistan. In this expanded sampling two individuals from Bangladesh were identical while the third was more closely related to the two from Pakistan. The two individuals from Pakistan differ from one another by a single base pair transition and differ from the third Bangladesh individual by two transitions. This low degree of observed genetic differentiation is consistent with our recognition of *C. indica* as a

TABLE 2: Sequence divergence for the outgroup taxa, *Pelochelys cantorii* and *P. bibroni*, and all *Chitra* individuals. The numbers of substitutions are above the diagonal; uncorrected P distances are below it. Reprinted from Engstrom et al. (2002).

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. <i>Pelochelys cantorii</i>	-	53	82	83	86	85	80	80	81	81	81	77	77
2. <i>P. bibroni</i>	0.072	-	87	88	93	92	87	87	88	88	88	94	94
3. <i>Chitra indica</i> Bangladesh	0.112	0.119	-	1	62	61	58	58	57	57	57	58	58
4. <i>C. indica</i> Bangladesh 2	0.113	0.120	0.001	-	63	62	59	59	58	58	58	59	59
5. <i>C. chitra chitra</i> Thailand	.118	0.127	0.085	0.086	-	1	8	8	7	7	7	39	39
6. <i>C. chitra chitra</i> Malaysia	0.116	0.126	0.083	0.085	0.001	-	7	7	6	6	6	38	38
7. <i>C. chitra javanensis</i> Sumatra 1	0.109	0.119	0.079	0.081	0.011	0.010	-	0	1	1	1	37	37
8. <i>C. chitra javanensis</i> Sumatra 2	0.109	0.119	0.079	0.081	0.011	0.010	0.000	-	1	1	1	37	37
9. <i>C. chitra javanensis</i> Java 1	0.111	0.120	0.078	0.079	0.010	0.008	0.001	0.001	-	0	0	38	38
10. <i>C. chitra javanensis</i> Java 2	0.111	0.120	0.078	0.079	0.010	0.008	0.001	0.001	0.000	-	0	38	38
11. <i>C. chitra javanensis</i> Java 3	0.111	0.120	0.078	0.079	0.010	0.008	0.001	0.001	0.000	0.000	-	38	38
12. <i>Chitra vandijki</i> Myanmar 1	0.105	0.128	0.078	0.081	0.053	0.052	0.051	0.052	0.051	0.052	0.052	-	0
13. <i>Chitra vandijki</i> Myanmar 2	0.105	0.128	0.078	0.081	0.053	0.052	0.051	0.051	0.052	0.052	0.052	0.000	-

monotypic species across its range (see Fig. 3B). This apparent genetic uniformity across such a broad geographic area, possibly explained by a highly mobile, riverine species being found in interconnected river systems, is an interesting biogeographic phenomenon, and merits further investigation (Engstrom and McCord, this volume).

We also confirm that for identification purposes, *Chitra* taxa show a fundamental division into two “phenotypic groups”. First is the “*Chitra indica* group” including *C. indica* and Myanmar *Chitra*, defined here as having: a very or relatively complex vertebral and costal pattern; a neck “V” with divergence point located on the anterior half of the extended neck; all neck stripes “blending” posteriorly into the carapacial and axillary areas; three to four forelimb lamellae; no continuous light rim on the carapace; no bell-like figure on the carapace; and no

distinct naso-orbital triangular figure. The other is the “*Chitra chitra* group” including Thai, Malaysian and Indonesian *Chitra*, having: a very or relatively simple vertebral and costal pattern; a neck “V” with divergence point located at or near the anterior border of the leathery carapace; neck stripes just lateral to the median neck stripe that continue posteriorly to form the continuous light rim present on the carapace; an average of two forelimb lamellae; a bell-like figure on the anterior carapace; and a distinct naso-orbital triangular figure (Table 3).

The molecular results (Figs. 6 - 7) do not parallel the “phenotypic groups” presented above. Genetically, Myanmar *Chitra* are closer to *C. chitra* than *C. indica*. This suggests that the phenotypic similarities between *C. indica* and Myanmar *Chitra* are shared ancestral character states (the “original” *Chitra* phenotype), and that the phenotypic differences in *C. chitra* would

TABLE 3: List of 14 diagnostic characters and their character states for the following species/subspecies of the genus *Chitra*: *C. indica*, *C. vandijki*, *C. chitra chitra*, *C. chitra javanensis*

	<i>C. indica</i>	<i>C. vandijki</i>	<i>C. c. chitra</i>	<i>C. c. javanensis</i>
1. Overall colouration	olive to deep-olive green	chocolate brown	greenish-yellow to olive-green	black
2. Midline (vertebral) carapacial pattern	very complex	moderately complex	simple	simple
3. Midline (vertebral) carapacial stripe	present	absent	usually present	absent
4. Radiating costal stripes	complex	simple	simple	simple
5. Paramedian neck stripes forming a bell-like pattern on anterior carapace	absent	absent	present	present
6. Neck stripes that form a continuous light rim around carapace	no	no	yes	yes
7. Distinct third pair of neck stripes	no	yes	no	no
8. Presence of dark speckling on “light” (head and neck) stripes	yes	no	no	no
9. Neck ‘V’ divergence point on neck	anterior	anterior	posterior	posterior
10. Number of forelimb lamellae	3-4	3-4	2	2
11. Peri-orbital ‘X’ pattern	no	no	no	yes
12. Distinct peri-orbital ocelli	no	yes	no (or partial)	no
13. Distinct naso-orbital triangular “figure”	no	no (or partial)	yes	yes
14. Chin pattern	Few, if any black dots present	black dots present	black dots present	black dots and ocelli present

then be autapomorphies. At one time a common Myanmar *Chitra* and *C. chitra* ancestor became isolated from their *C. indica* ancestor, only later again to become isolated from each other. This allows *C. indica* and Myanmar *Chitra* to maintain a phenotypic resemblance to their common ancestor and thus each other, while at the same time allowing *C. chitra* to be phenotypically different from Myanmar *Chitra*, even though they share a common ancestor more recently. We must also consider that since DNA analysis only looks at part of the total genome, it is possible there are phenotypic differences for which the genetic basis has not yet been identified.

The various, parallel lines of investigation described in this paper, that include zoogeographic, morphological, chromatic, and genetic approaches, converge upon the conclusion that softshell turtles of the genus *Chitra* from Myanmar constitute an undescribed new species, and that *Chitra chitra* from eastern Java are subspecifically distinct. Descriptions and hypodigm are given in the text below.

Chitra indica (Gray 1831a) Indus, Ganga, Brahmaputra, and several peninsular river systems in India. See Appendix I for chresonymy.

Dorsal pattern (Fig 8A): The overall colour of the dorsal disc (carapace) varies greatly, from pale buff to typically deep olive green, and this variation is evident even among very young specimens. The overall pattern of juveniles is characterized by numerous elongate, irregular, curved light markings. These figures are asymmetrical and dark-bordered; they have a tendency towards longitudinal extension along the vertebral area, and radial deployment along the costals and towards the periphery. Dark spots, small blotches and ocelli may be dispersed among these wandering, vermiform markings. Around the periphery, the light markings may be relatively small and truncated by the edge of the leathery disc. At no stage is there a pale border to the entire outer circumference of the carapace in this species. Anteriorly, the markings become more organized and extend forward into the characteristic longitudinal dorsal neck stripes, the paramedian pair of which meet mesially behind the level of the skull.

With growth, the markings change. In the costal area, the markings radiating towards the periphery may become complex, and give the impression of a palimpsest of bold, dark-bordered vermiform figures superimposed upon a layer of much less defined "shadow" markings. Changes also occur in the vertebral region, where, in turtles of 15-18 cm or greater size, a remarkable, complex design of straight-edged, geometric figures develops. This design includes a pair of distinct, although sometimes interrupted, longitudinal light markings enclosing a series of finely-wrought triangular figures, oblique lines, and very fine longitudinal lines. A fine, sometimes interrupted, distinct midline stripe originating at the anterior rim of the bony carapace is usually present.

In large animals, the markings fade first along the midline, spreading to encompass the area of the bony disc, and ultimately the pattern fades over the entire leathery disc. By contrast, in the related giant softshell *Pelochelys bibroni* from southern New Guinea, which has dorsal markings similar to those of *Chitra* (although lacking the neck "V"), it appears that the pattern is poorly developed in young specimens, but is very bold and striking in large individuals (Webb, 1995).

Ventral coloration: The plastron is unpigmented, white in colour, sometimes with a pink tinge (vascular "blushing") in live individuals. The underside of the limbs and neck usually have a yellowish tinge. The only areas of the ventral aspect that are pigmented are the soles of the feet, which are varying shades of gray. The dorsal surface of the tail is light gray.

Cephalic and Neck Pattern (Figs. 9A & 10A): The most obvious component of the head and neck pattern is the series of longitudinal stripes, of which there are four on the dorsal surface of the head. The base of the neck has a pair of paramedian stripes that connect into a "V" anteriorly to form a single median stripe. There are two other pairs of stripes on the neck lateral to the paramedian stripes at the base of the neck and to the median stripe on the anterior neck. The most lateral pair blends posteriorly into the axillary region, while the inner pair blends posteriorly into the carapacial pattern (versus continuing intact

around the entire rim of the carapace in *C. chitra*). Some individuals display a very indistinct third pair of stripes lateral to all others in the anterior neck. The distinct light stripes are dark bordered, typically with dark speckling within the stripes, and usually heavier dark speckling between them. The paramedian neck stripes extend posteriorly onto the carapace, where they become vaguely incorporated into the carapacial markings. The junction of the paramedian neck stripes (neck “V”) occurs far forward on the anterior half of the extended neck, with the distance from the junction of the “V” to the anterior edge of the bony carapace (disc) being approximately 25% of the length of the entire carapace. In rare cases, the paramedian stripes may terminate at a transverse bar before reaching the junction of the “V”, or they may become conjoined halfway along the neck, in all cases re-separating transversely near the back of the head. The pattern between the eyes consists of dark speckles only. The irides are golden yellow. The chin bears few, if any black dots. There is no distinguishable naso-orbital stripe pattern.

Chitra vandijki sp. nov.

See Appendix I for chresonymy.

Holotype: PCHP (CRI) 7059, a 22.0 cm (CL) subadult in alcohol, from the Ayeyarwaddy River system, northeastern Myanmar (Fig. 11). Obtained in the Ruili (Yunnan, China) market by O. Shiu, in 1997.

Paratypes: PCHP (CRI) 4896, a 41.2 cm subadult and PCHP (CRI) 4897, a 23.0 cm subadult, both in alcohol. PCHP (CRI) 5050, a 36.8 cm (bony disc length) subadult skeleton. All have same collection data as holotype.

Vernacular Name: Myanmar Narrow-Headed Softshell Turtle.

Etymology: Named in honor of Peter-Paul van Dijk, of the Netherlands, the University of Galway in Ireland, and Chulalongkorn University in Bangkok, in recognition of his noteworthy contributions to the science and conservation of turtles and tortoises, especially the trionychid turtles of Asia.

Type locality: Since the holotype specimen has no specific locality, we hereby designate the type locality as Khayansat Kone Village

(23°16.30'N; 95°58.99'E) on the Ayeyarwaddy River, where the species was first collected with precise field data by Steven Platt, 2001.

Distribution: The Ayeyarwaddy River basin of Myanmar. Not occurring sympatrically with any other *Chitra*.

Diagnosis and Diagnostic Comparisons: A large softshell turtle of the genus *Chitra*, in the *Chitra indica* “phenotypic group”, distinguished from members of the *Chitra chitra* “phenotypic group” (Thai, Malaysian and Indonesian *Chitra*) by having: a relatively complex vertebral and costal pattern; a neck “V” with divergence point located on the anterior half of the extended neck; paramedian neck stripes blending into the carapacial pattern and not forming a bell-like figure near the front of the carapace; three to four forelimb lamellae; no continuous light rim around the carapace; and no distinct naso-orbital triangular “figure”.

Chitra vandijki is distinguished from *C. indica*, the other recognized member of the *Chitra indica* “phenotypic group” by having: a wider bony shell; distinctly wider neural bones (see above); a more abruptly terminating, thicker-edged bony carapace; larger, wider, and less tapered rib tips extending beyond the bony carapace; an overall chocolate brown coloration; no midline carapacial stripe; less overall complexity to the vertebral and costal patterns; a distinct third pair of neck stripes lateral to the median stripe of the neck; distinct ocelli between or behind the eyes; no dark speckling on the light head and neck stripes; and black speckling on the chin.

Description: Dorsal pattern (Fig. 8B): The overall dorsal coloration is considerably darker than that of Indian specimens, with chocolate-brown and yellow-ochre colours predominating. The vertebral markings are relatively simplified, lacking the triangular and oblique elements, and the distinct midline stripe of *C. indica*. The streaks over the costal bones are markedly asymmetrical in most individuals, showing little if any “fine structure” or shadow-markings between the bold streaks. The leathery peripheral area of the dorsal disc is sprinkled predominantly with heavy, generally

shapeless light blotches, some subcircular, others less vermiform than in *C. indica*, and with “finer” dark speckling between these light blotches than in *C. indica*. We have not seen very large specimens, and thus cannot comment on ontogenetic changes in pigmentation. Our largest live specimen has a total dorsal disc length of 38.5 cm. Platt (2001) illustrated a 40.8 cm specimen with coloration similar to those in our series.

Ventral coloration: The plastron is white or pinkish. The ventral surface of the limbs and neck have a yellowish tinge. The soles of the feet and dorsal surface of the tail are mid-gray to almost black in colour.

Cephalic and Neck pattern (Figs. 9B - 10B): Because of the dark background colour, the dark borders of the four dorsal head stripes and the speckling in between the stripes are less contrasting than in *C. indica*. The speckling is absent within the dark borders of the light stripes of both head and neck. The dorsal neck markings include the standard “V” composed of the convergent paramedian stripes, with the apex of the “V” located on the anterior half of the extended neck at a distance from the anterior of the bony carapace (disc) approximating 20% of the entire carapace length. In this taxon, there are three well-defined, black-bordered stripes on the anterior part of the neck lateral to the median stripe on each side, giving a total of seven distinct stripes at this location on the neck (5 in *C. indica*). As in *C. indica*, the cranial median neck stripe bifurcates transversely near the back of the head. The stripes are often asymmetrical, contorted, or abruptly truncated, and may show asymmetrical lateral cross-connections. The paramedian neck stripes blend posteriorly into the carapacial pattern. The adjacent pair end abruptly on the carapacial rim between the neck and the forelimbs. The most lateral pair of lower (posterior) neck stripes blend into the axillae, while the most lateral (third) pair on the upper (anterior) neck, blend into the ventral mid-neck area. The interorbital pattern is very distinctive, usually including both a transverse light, dark-bordered bar connecting the orbits and one or two pairs of entire or nearly entire light, dark bordered ocelli posterior to the transverse bar between, or behind the eyes. The

irides are bright golden-yellow, the chin is speckled with black and a naso-orbital figure is absent or poorly defined.

Chitra chitra chitra Nutaphand, 1990. Thailand (Khwae, Mae Klong and Mae Ping River systems) and Peninsular Malaysia.

See Appendix I for chresonymy.

Dorsal pattern (Fig. 8C): In Thai specimens, the predominant dorsal coloration in younger (up to 40 cm) specimens is varying shades of greenish-yellow. The background coloration darkens to olive green with growth, and large adults may be almost black, although the light markings remain distinct. In young animals, the leathery (dorsal) disc has a rather simple, although usually asymmetrical, pattern, with wandering, sometimes branched, vermiform, light, dark-bordered markings that in general become smaller towards the periphery. There is often a median vertebral stripe originating over the anterior bony carapace, no indistinct “shadow” markings, and the adornments of the vertebral area are not set-off or distinct in any way from those on the costals. Sometimes two distinct discontinuous paramedian vertebral stripes are also present, contrasting with the complex vertebral pattern of *C. indica*. The margin of the carapace is outlined with a light, continuous ring. In some individuals, the bold pale dorsal markings are sharply angular or hatchet-shaped rather than vermiform. The degree to which their form may change with ontogeny is not clear. In our experience the pattern is similar in specimens 30-75 cm in carapace length.

Ventral coloration: The plastron is unpigmented, the undersides of the limbs and neck may have a yellowish tinge, and the soles of feet and dorsal side of the tail are dark.

Cephalic and Neck pattern (Figs. 9C - 10C): Four longitudinal head stripes are present. The paramedian neck stripes converge anteriorly to form the neck “V” much more posterior than in Myanmar specimens or in *C. indica*, typically at a point separated from the anterior of the bony carapace (disc) by a distance of only 10-12% of the length of the entire carapace. As paramedian neck stripes continue posteriorly they diverge on the carapace and form laterally-spreading curves

or “hooks” that usually extend to reach the carapace margin anterolaterally. They display an angular medial constriction close to the point where they pass over the anterior bony disc, producing an indistinct bell-shaped figure. The pair of neck stripes adjacent to the median neck stripe diverge posterolaterally when reaching the anterior leathery carapace and each becomes continuous with the light border of the entire leathery carapace. The most lateral distinct neck stripes posteriorly blend into the axillary region. The anterior neck displays a third poorly defined pair of lateral neck stripes. The median neck stripe bifurcates transversely behind the head. No dark speckling is present in the light areas within the dark borders of the head and neck stripes. Dorsally, the orbits are connected by one or two transverse bars, sometimes with irregular and incomplete ocelli between or behind the eyes that connect to the anterior paramedian head stripes. When present these partial ocelli are not as distinct as in the Myanmar form. The irides are golden yellow. The chin has black ventral speckling. The naso-orbital pattern is very distinct, composed (in young specimens) of three light, dark-bordered stripes from nostrils to eyes, and from eye to eye, forming an anteriorly pointed triangular pattern. In larger specimens this nose/eye “figure” becomes a solid (anteriorly directed) light triangle.

Chitra chitra javanensis ssp. nov.

See Appendix I for chresonymy.

Holotype: MZB 199, a 57.0 cm (CL), dried specimen, captured July 1997 in a tidal creek of the Pasuruan River, near Pasuruan, East Java, Indonesia by local turtle hunters. Donated by F. Yuwono (Fig. 12).

Paratypes: MZB 264, a 34.2 cm subadult and MZB 265, a 15.5 cm juvenile, both in alcohol; MZB 266 and 267, both subadult skeletons; PCHP (CRI) 4965, a 32.3 cm subadult in alcohol and PCHP (CRI) 4975, an adult skeleton, bony disc length 48.0 cm; RMNH 34920, a 32.5 cm subadult and RMNH 34921, a 35.2 cm subadult, both in alcohol, and donated by H-D Philippen. All have same collection data as holotype.

Vernacular Name: Java Narrow-Headed Softshell Turtle.

Etymology: Based upon the locality where the type specimens were collected (see text).

Type locality: Pasuruan River drainage, near Pasuruan, Probolinggo District, East Java, Indonesia.

Distribution: Currently known from the Pasuruan and Solo River drainages of eastern and central Java, Indonesia (see text for additional localities). *Chitra c. javanensis* is not sympatric with any other species or subspecies of *Chitra*.

Diagnosis: A large softshell turtle of the genus *Chitra*, a member of the *Chitra chitra* “phenotypic group”, is distinguished from members of the *Chitra indica* “phenotypic group” (*C. indica*, *C. vandijki*) by having: a reduced, simple vertebral and costal pattern; a neck “V” located at or near the anterior rim of the leathery carapace; an average of 2 forelimb lamellae; a very distinctive bell-like design on the anterior carapace; a continuous light circumferential rim on the leathery carapace, continuing anteriorly as neck stripes just lateral to the paramedian and median neck stripes; and a distinct triangular naso-orbital “figure”.

Chitra c. javanensis is distinguished from the nominate subspecies (*Chitra c. chitra*) and fellow member of the *Chitra chitra* “phenotypic group” by having: darker overall coloration, especially in younger specimens; midline and lateral vertebral carapacial stripes usually lacking; a much more distinctive bell-shaped “figure” on the anterior of the carapace; an “X” shaped figure between the eyes formed by the anterior paramedian head stripes; no partial ocelli between or behind the eyes; bolder black speckling and ocelli on the chin; and narrower, more elongate costal markings.

Description: Dorsal pattern (Fig. 8D): The overall dorsal coloration is dark olive-brown to black, the light markings being light yellow-brown. The pale markings of the carapace, especially peripherally, are fewer in number and of smaller vermiform design, when compared to the more numerous and bolder vermiform markings of Thai and Malaysian specimens, and are often only pale “blotches”. A median, and less often lateral, discontinuous vertebral stripes are all infrequently present over the bony carapace. The

carapacial margin is outlined with a light, continuous ring. A distinctive bell-like design is seen on the anterior of the leathery carapace. There are no indistinct “shadow” markings, and neither the vertebral nor costal areas have complex designs as in *C. indica*.

Ventral Coloration: The plastron is unpigmented; the underside of the limbs and neck are often yellow-tinged; the soles of the feet are dark, as is the dorsal tail.

Cephalic and Neck pattern (Figs. 9D & 10D): Four longitudinal head stripes are present. The paramedian head stripes continue anteriorly decussating between or just behind the eyes so as to form an “X” pattern, and terminate at the anteromedial border of the opposite eye. As the median neck stripe posteriorly crosses the anterior leathery carapace it divides to form the neck “V”. The point of divergence of the median neck stripe is posteriorly located as in Thai and Malaysian specimens. From this point these light stripes continue caudolaterally, until at the level of the anterior bony disc they briefly angle inward, sometimes almost meeting on the midline over the nuchal bone, before diverging toward the anterolateral rim of the carapace. This pattern usually leaves a distinct bell-like design. The pair of neck stripes adjacent to the paramedian neck stripes posteriorly diverge when reaching the anterior leathery carapace and each becomes continuous with the light border of the entire carapace. The most lateral distinct neck stripes blend into the axillae. The anterior neck displays a third poorly defined pair of lateral neck stripes. The median neck stripe bifurcates transversely behind the head. No dark speckling is present in the light areas within the dark borders of the head and neck stripes. The irides are golden yellow, the ventral chin has both strong black speckling and light centered black ocelli, and the naso-orbital stripe pattern is present, as in Thai and Malaysian forms. With growth the “triangular” figure between the eyes and nose (originally

light stripe bordered with a dark center) becomes uniformly light in colour.

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APPENDIX I

The following chronological chresonymy (Smith and Smith, 1973) presents original descriptions, synonyms, authors, dates and pagination of first use authorship for the narrow-headed softshell turtles of the genus *Chitra* and is the result of reviewing (with citation) the reference list herein. Authors of original descriptions are indicated by lack of colon or parentheses in the nominal-complex (Dubois, 2000). The type locality along with data for all available types is given. "In part" connotes inappropriate synonymy (= inapp. syn.) and that the author(s) included other forms (correctly or incorrectly) under the same name at that time. Explanation for names not presently in use is given. A bracketed [] nominal-complex is the currently accepted genus and species for that given synonym.

Chitra indica (Gray 1831a)

Trionyx Indicus Gray, 1831a: 18. Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]). Type locality is stated as "India" in Gray (1831a), "Ganges" on Plate 80, revised to "India: Ganges; Futtaghur" by Gray (1864:92), later again revised to "Fatehgahr, Ganges" by Smith (1931: 162), accepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." Objectively synonymized as "*Trionyx Indicus*, Gray, *Syn. Rept.* 47" under *C. indica* (Gray, 1831a:18) by Gray (1844: 49). [= *C. indica* (Gray, 1831a: 18)].

Trionyx Egyptiacus, Var. [sic] *Indicus* Gray, 1831a: Gray (1831b: 47; in part, includes Ganges and Barrackpore, India and Penang, Malaysia in locality data). Presently treated as an objective synonym (same type). Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]). Type locality: originally "India" in Gray (1831a); stated as "In India, fl. Ganges, Penang" in Gray (1831b), revised to "India: Ganges; Futtaghur" by Gray (1864:92), later again revised to "Fatehgahr, Ganges" by Smith (1931: 162), accepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." Inapp. syn. as ssp. of *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, 1809: 12 (= *nomen substitutum* (Wermuth and Mertens, 1961: 282) for *Testudo triunguis* Forskål, 1775: 17). Synonymized under *Trionyx indicus* Gray, 1831a: 18 by Gray (1831b: 47). [= *C. indica* (Gray, 1831a: 18)].

Testudo Chitra Buchanan-Hamilton (unpublished): Gray (1831b: 47; in part, includes Ganges and Barrackpore, India and Penang, Malaysia in locality data). Illustration drawn 1804-5, # 522 India Office, London. Declared *nomen nudum* by Wermuth and Mertens (1961) since only published as a synonym, with no description, and not treated as an independent taxon before 1961 (ICZN Code). Type locality: specimens collected in India, Nepal and Burma were painted in Barrackpore, India (Archer, 1962: 39, 72); stated as "In India, fl. Ganges, Penang" in Gray (1831b), revised to "India: Ganges; Futtaghur" by Gray (1864:92), later again revised to "Fatehgahr, Ganges" by Smith (1931: 162), accepted by Webb (1980: 72) and us as "Fategarh on the river Ganges, India." Subjectively synonymized under *Trionyx indicus* Gray, 1831a:18, by Gray (1831b: 47). [= *C. indica* (Gray, 1831a: 18)].

Testudo membranacea Blumenbach, 1779: Gray (1831b: 47, referring to "Mus. Col. Surg." specimen #1238.B; in part, includes Ganges and Barrackpore, India and Penang, Malaysia in locality data). *Nomen dubium* (available evidence is insufficient to permit recognition of the species to which this name was applied). Holotype: None designated. Type locality: "Guiana", South America (= *ex errore*). Questionable synonymy under *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, 1809:12 by Schweigger (1812: 366); *Trionyx indicus* Gray, 1831a:18, by Gray (1831b: 47); and *Trionyx cartilaginea* (Boddaert, 1770) by Wermuth and Mertens (1961: 263). [= possibly *Amyda cartilaginea* (Boddaert, 1770: 1-39)].

TRIONYX AEGYPTIACUS. Var. *Indica* Gray, 1831a: Gray (1831 ["1830-35"]) Plate 80 in *Illus. Ind. Zool.* (1): "part" 8, see Sawyer 1971: 50; Webb, 1980: 62). [See as "*Trionyx Aegyptiacus*, var. *Indica*" on second introductory page, Gray (1830-35) *Illus. Ind. Zool.*, R. Webb, pers. comm.]. Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]). Type locality: originally "India" in Gray (1831a); stated as "Ganges" on Plate 80, revised to "India: Ganges; Futtaghur" by Gray (1864:92), later again revised to "Fatehgahr, Ganges" by Smith (1931: 162), accepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." Inapp. syn. as ssp. of *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, 1809: 12 (= *nomen substitutum* (Wermuth and Mertens, 1961: 282) for *Testudo triunguis* Forskål, 1775: 17). Objective synonymy under *Trionyx indicus* Gray 1831a:18 prior to publication of Plate 80 (see Webb, 1980: 62, 70), by Gray (1831b: 47). [= *Chitra indica* (Gray, 1831a: 18)].

Gymnopus lineatus Duméril and Bibron, 1835: 491. Holotype: MNHN 6968. Type locality: "le Gange" river, India, later revised to "India: Ganges; Futtaghur" by Gray (1864:92). Conditionally and subjectively synonymized in Duméril & Bibron (1835: 492) with Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]), and *T. indicus* in Gray (1831b: 47). Subjectively synonymized with "*Trionyx Indicus*, Gray, *Syn. Rept.* 47" under *Chitra indica* (Gray, 1831a:18) by Gray (1844: 49). [= *Chitra indica* (Gray, 1831a: 18)].

Trionyx Aegyptiacus, var. *Indicus* Gray, 1831a: Gray (1844: 49; in part, includes India, Philippine Islands, and Penang, Malaysia in locality data, [Synonym not italicized in original work here, nor in Gray 1855:70 with same improper spelling (letter case); correctly italicized and proper case as *Trionyx aegyptiacus*, var. *indicus* in Gray 1864:91, 1872:332, 1873:41; proper case, but italicized incorrectly as *Trionyx aegyptiacus*, var. *indicus* in Gray 1870:89; proper case, with nothing italicized (with publication date of Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"])) incorrectly given as "1832") as *Trionyx aegyptiacus*, var. *indicus* in Boulenger (1889:264)]. Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]). Type locality: originally "India" in Gray (1831a), stated as "Ganges" on Plate 80, as both "Philippine Islands" and "India" in Gray (1844:49), revised to "India: Ganges; Futtaghur" by Gray (1864:92), again revised to "Fatehgahr, Ganges" by Smith (1931: 162), ac-

cepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." Inapp. syn. as ssp. of *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, 1809: 12 (= *nomen substitutum* (Wermuth and Mertens, 1961: 282) for *Testudo triunguis* Forskål, 1775: 17). Objective synonymy under *Trionyx indicus* Gray 1831a:18 (see Webb, 1980: 62, 70) by Gray (1831b: 47). [= *Chitra indica* (Gray, 1831a: 18)].

Chitra indica (Gray, 1831a): Gray (1844: 49; in part, includes India, Philippine Islands, and Penang, Malaysia in locality data; synonym not italicized in original work). Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]). Type locality: originally "India" in Gray (1831a); stated as both "Philippine Islands" and "India" in Gray (1844: 49), revised to "India: Ganges; Futtaghur" by Gray (1864:92), later again revised to "Fatehgahr, Ganges" by Smith (1931: 162), accepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." [= *C. indica* (Gray, 1831a: 18)].

Gymnopus indicus (Gray, 1831a): Cantor (1847: 10, 616; in part, includes "Pinang, Malayan Peninsula, (Estuaries, Sea Coast). Rivers in India, Philippine Islands" in locality data; synonym not italicized in original work). Holotype (for synonym): RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]); but here used by Cantor (1847) is BMNH 1947.3.6.21, stuffed subadult, and BMNH 1947.3.6.22, skull from same specimen (see Boulenger 1889:263 cite same BMNH specimens as "a. Hgr. [half grown], stffid., skull separate. Pinang. Dr. Cantor. (Type.)" under *P. cantoris* [= *P. cantorii* Gray, 1864: 90]). Type locality (for synonym): originally "India" in Gray (1831a); stated as quoted above in Cantor (1847), revised to "India: Ganges; Futtaghur" by Gray (1864:92), later again revised to "Fatehgahr, Ganges" by Smith (1931: 162), accepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." Cantor, unaware of the then undescribed genus *Pelochelys*, incorrectly synonymized his "Pinang" specimen with "Chitra indica, Gray: Catal." (= Gray, 1844:49); see footnote in Cantor (1847:616) "In the living adult no ... is apparent, nor the outline of the costae, as represented in the figure [Plate 80] in *Illustrations of Indian Zoology*". The synonym itself was objectively synonymized under "CHITRA INDICA. (Plate VI. fig. C. [thought to be a *P. cantorii* Gray, 1864: 90, with an erroneous *Chitra* pattern])" by Günther (1864: 50). [= *C. indica* (Gray, 1831a: 18)].

Pelochelys cantorii Gray, 1864: 90; in part, due to synonymy here with "*Chitra indica*" (Gray, 1831a: 18) and "*Gymnopus indicus*" (Gray, 1831a: 18); synonym not italicized in original work. Holotype: Jointly BMNH 1947.3.6.21, stuffed subadult, and BMNH 1947.3.6.22, skull (see Figs. 9 and 10) from same specimen (see reference here to Cantor (1847) specimen); also see Boulenger's (1889:263) [Cantor (1847)] specimen "a" as "Type". Type locality: here as "Malacca" (Malaysia); includes India, Penang, Malaysia and Philippines in locality data through synonymy; revised to "all other [excluding New Guinea] *Pelochelys* populations" by Webb (1995:308). Inapp. syn. with Günther's (1864: 50) erroneously illustrated (see text) "*Chitra indica*" [although stated "not Gray", meaning here, not *Chitra indica* (Gray,

1831a:18)] by Gray (1864: 90), and under *Trionyx* (*Gymnopus*) *Bibroni* Owen, 1853:185, by Günther (1864: 108), Smith (1931: 160) and Wermuth and Mertens (1961: 260). See Webb (1995: 308) for proper designation. [= *Pelochelys cantorii* Gray, 1864: 90].

Pelochelys cumingii Gray, 1864: 90; in part, due to synonymy here with "*Chitra indica*" (Gray, 1831a: 18); synonym not italicized in original work. Note incorrect subsequent spelling (*P. cumingii*) in Smith (1931: 160). Holotype: none designated. Syntypes (see inapp. syn. with *C. indica* (Gray 1831a: 18), as "a" and "b" in Gray (1844: 49); see also same specimens "f" and "g" designated by Boulenger (1889: 263) as "Types of *P. cumingii*"): BMNH 1947.3.4.5 and BMNH 1946.1. 22.13. Type locality: here as "Philippines"; includes India, Penang, Malaysia and Philippines in locality data through synonymy. Inapp. syn. with "*Chitra indica*, *Gray, Cat. Tort. B. M.* 49" by Gray (1864: 90, see reference to "Gray, Cat. Shield Rept. B.M. p. 70"). Proper synonymy under *Pelochelys cantoris* [sic, = *P. cantorii* Gray, 1864:90], but inapp. syn. with "*Chitra indica*, part., *Gray, Cat. Tort. P.* 49 (1844)" by Boulenger (1889: 263). Properly synonymized with *P. cantorii* Gray, 1864: 90, but inapp. syn. under *P. bibroni* (Owen, 1853: 185) by Smith (1931: 160), and Wermuth and Mertens (1961: 260). See proper subjective synonymy ("line priority") under *Pelochelys cantorii* Gray, 1864: 90, by Webb (1995: 308). [= *Pelochelys cantorii* Gray, 1864: 90].

Trionyx lineatus (Duméril and Bibron, 1835): Martens (1876: 196; in part, includes both India and Philippines in locality data; synonym not italicized in original work). Holotype: MNHN 6968. Type locality: originally "le Gange" by Duméril and Bibron (1835); stated as "Philippinischen Inseln" (Philippine Islands) in Martens (1876). Conditionally and subjectively synonymized in Duméril & Bibron (1835: 492) with Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]), and *T. indicus* in Gray (1831b: 47). Inapp. syn. here placing Philippine *P. cantorii* Gray, 1864:90 under *Trionyx* (*Gymnopus*) *lineatus* (Duméril and Bibron, 1835). See also inapp. syn. under "Philippinen" *C. indica* var. [sic] *cumingi* (= *P. cantorii* Gray, 1864:90) by Boettger (1886: 93). Subjectively synonymized with "*Trionyx Indicus*, *Gray, Syn. Rept.* 47" under *Chitra indica* (Gray, 1831a:18), by Gray (1844: 49). [= *Chitra indica* (Gray, 1831a: 18)].

Chitra Indica var. [sic] *Cumingi* (Gray, 1864): Boettger (1886: 93; in part, includes India, Nepal, Penang, Malaysia and Philippines in locality data). Holotype: none designated. Syntypes (see inapp. syn. with *C. indica* (Gray 1831a: 18), as "a" and "b" in Gray (1844: 49); see also same specimens "f" and "g" designated by Boulenger (1889: 263) as "Types of *P. cumingii*"): BMNH 1947.3.4.5 and BMNH 1946.1.22.13. Type locality: originally "Philippinen" in Gray (1864:90). Inapp. syn. as ssp. of *C. indica* (Gray, 1831a: 18). Inapp. syn. with "*Chitra indica*, *Gray, Cat. Tort. B. M.* 49" by Gray (1864: 90, see reference to "Gray, Cat. Shield Rept. B.M. p. 70"). Proper synonymy under *Pelochelys cantoris* [sic, = *P. cantorii* Gray, 1864:90], but inapp. syn. with "*Chitra indica*, part., *Gray, Cat. Tort. p.* 49 (1844)" by Boulenger (1889: 263). Properly synonymized with *P. cantorii* Gray, 1864: 90, but inapp. syn. under *P. bibroni* (Owen, 1853:185) by Smith (1931: 160), and Wermuth and Mertens (1961: 260). See

proper subjective synonymy ("line priority") under *Pelochelys cantorii* Gray, 1864: 90 by Webb (1995: 308). [= *Pelochelys cantorii* Gray 1864: 90].

Pelochelys cantoris [sic] Gray, 1864: Boulenger (1889: 263; in part, due to synonymy here with "*Chitra indica*" (Gray, 1831a:18), "*Gymnopus indicus*" (Gray, 1831a:18) and "*Pelochelys bibronii*" (Owen, 1853: 185, 207); synonym not italicized in original work). Holotype: Jointly BMNH 1947.3.6.21, stuffed subadult, and BMNH 1947.3.6.22, skull from the same specimen (here as Cantor's specimen "a", identified as the "Type"). Type locality: originally "Malacca" in Gray (1864:90); stated here as "Ganges, Burma, Malay Peninsula, Borneo, Philippines"; revised to "all other [excluding New Guinea] *Pelochelys* populations" by Webb (1995:308). Declared "an unjustified emendation" of *P. cantorii* Gray, 1864: 90 by Webb (1995: 308), and an incorrect subsequent spelling by us. Inapp. syn. here with "*Chitra indica*, part., *Gray, Cat. Tort. P.* 49 (1844)". [= *Pelochelys cantorii* Gray, 1864: 90].

Pelochelys bibronii (Owen, 1853): Boulenger (1889: 263; in part, includes "Ganges, Burma, Malay Peninsula, Borneo, Philippines" in locality data; synonym not italicized in original work). Incorrect subsequent spelling. Holotype: Jointly RCS (London) 954-959 and 1093-1094, a group of skull and other skeletal parts from one specimen (see Webb, 1995: 301) – all lost in WW II. Neotype: AMS 3425, designated by Webb (1995: 302). Type locality: originally "Australian" [ex errore, by Owen (1853) and Gray (1864)]; stated as quoted above by Boulenger (1889), revised to "southern New Guinea" by Webb (1995: 302). Inapp. syn. here with "*Chitra indica*, part., *Gray, Cat. Tort. P.* 49 (1844)". [= *Pelochelys bibroni* (Owen, 1853: 185, 207)].

Trionyx aegyptianus, var. *indicus* Gray, 1831a: Boulenger (1890:16; in part, includes "Ganges and Irrawaddy" and Penang (Malaysia, through synonymy) in locality data; synonym not italicized in original work). Incorrect subsequent spelling. Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]). Type locality: originally "India" in Gray (1831a); stated as "Ganges" on Plate 80, revised to "India: Ganges; Futtaghur" by Gray (1864:92), as given above by Boulenger (1890:16), later again revised to "Fatehgahr, Ganges" by Smith (1931: 162), accepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." Inapp. syn. as ssp. of *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, 1809: 12 (= *nomen substitutum* (Wermuth and Mertens, 1961: 282) for *Testudo triunguis* Forskål, 1775:17). Objective synonymy under *Trionyx indicus* Gray, 1831a:18 (see Webb, 1980: 62, 70) by Gray (1831b: 47). [= *Chitra indica* (Gray, 1831a: 18)].

Pelochelys bibroni (Owen, 1853): Smith (1931: 160, 161; in part, includes "? Bengal; the Indo-Chinese Peninsula and Southern China; Hainan; ? the Malay Peninsula; Sumatra; Borneo; the Philippine Islands; New Guinea" in the locality data; synonym not italicized in original work; see also reference to "Australia" [ex errore, by Owen (1853) and Gray (1864)], under *Trionyx* (*Gymnopus*) *bibroni* Owen, 1853:185). Holotype: Jointly RCS (London) 954-959 and 1093-1094, a group of skull and other skeletal parts from one specimen (see Webb, 1995: 301) – all lost in WW II. Neotype:

AMS 3425, designated by Webb (1995: 302). Type locality: originally “Australian” (see above) by Owen (1853:185); stated as quoted above by Smith (1931: 161), later revised to “southern New Guinea” by Webb (1995: 302). Inapp. syn. here with “*Chitra indica* (in part) Günther 1864, p. 50, pl. vi.”, thought to represent a *P. cantorii* Gray, 1864:90 erroneously bearing a *Chitra* pattern. [= *Pelochelys bibroni* (Owen, 1853: 185, 207)].

Pelochelys poljakowii Strauch, 1890: Smith (1931: 160, 161; in part, includes “? Bengal; the Indo-Chinese Peninsula and Southern China; Hainan; ? the Malay Peninsula; Sumatra; Borneo; the Philippine Islands; New Guinea” in the locality data). Species name correctly emended here to lower case. Holotype: none designated by Strauch (1890). Syntypes: Strauch (1890: 18) lists two skeletal specimens (#’s 7896 and 7897) in the Zool. Inst., Russian Acad. of Sci., St. Petersburg (= ZISP). Type locality: “Fu-tschau” [= Fuzhou, Fujian Prov., see Zhao and Adler (1993: 431)], China by Strauch (1890); as quoted above by Smith (1931:161). Proper subjective synonymy with *P. cantorii* Gray, 1864:90, but inapp. syn. here with the name “*Chitra indica* (in part) Günther 1864, p. 50, pl. vi.”, even though thought to represent a *P. cantorii* Gray, 1864:90, erroneously bearing a *Chitra* pattern taken from Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]), see text. [= *Pelochelys cantorii* Gray 1864: 90].

Trionyx indica Gray, 1831a: Taylor (1970: 152; in part, gives “Fategarh, Ganges ‘Northern India’”, but through synonymy also Penang, Malaysia and Philippines included in locality data). Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]). Type locality: originally “India” in Gray (1831a); stated as “Ganges” on Plate 80, revised to “India: Ganges; Futtaghur” by Gray (1864:92), later again revised to “Fatehgahr, Ganges” by Smith (1931: 162), as quoted above by Taylor (1970), accepted by Webb (1980: 72) and us as “Fatehgahr on the river Ganges, India.” Proper objective synonymy as “*Trionyx Indicus*, Gray, *Syn. Rept.* 47” under *C. indica* (Gray, 1831a:18), by Gray (1844: 49). [= *C. indica* (Gray, 1831a: 18)].

Trionyx Aegyptianns [sic], var. *Indica* Gray, 1831a: Webb (1980: 63; typographical error for *Trionyx Aegyptiacus*, var. *Indica* on second introductory page, Gray (1830-35) *Illus. Ind. Zool.*, R. Webb, pers. comm.). Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]). Type locality: originally “India” in Gray (1831a); stated as “Ganges” on Plate 80, revised to “India: Ganges; Futtaghur” by Gray (1864:92), later again revised to “Fatehgahr, Ganges” by Smith (1931: 162), accepted by Webb (1980: 72) and us as “Fatehgahr on the river Ganges, India.” Inapp. syn. as ssp. of *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire 1809:12 (= *nomen substitutum* (Wermuth and Mertens, 1961: 282) for *Testudo triunguis* Forskål 1775: 17). Objective synonymy under *Trionyx indicus* Gray, 1831a:18 (see Webb, 1980: 62, 70) by Gray (1831b: 47). [= *Chitra indica* (Gray, 1831a: 18)].

***Chitra vandijki* sp. nov.**

Chitra Indica (Gray, 1831a): Theobald (1876: 27; in part, includes “the Ganges, Bengal, the Irawadi, and the estuaries

of the Indian and Malayan coasts” in the locality data; synonym not italicized in original work). See also Theobald (1882: 340); Boulenger (1889: 263,264); Annandale (1912: 152); Smith (1922: 264); Wermuth and Mertens (1961: 247); Taylor (1970: 153). Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]). Type locality: originally “India” in Gray (1831a); stated as both “Philippine Islands” and “India” in Gray (1844: 49), as “India: Ganges; Futtaghur” by Gray (1864:92), as quoted above by Theobald (1876: 27), later again revised to “Fatehgahr, Ganges” by Smith (1931: 162), accepted by Webb (1980: 72) and us as “Fatehgahr on the river Ganges, India.” Inapp. syn. with “Irawadi” *Chitra*. [= *C. indica* (Gray, 1831a: 18)].

Testudo chitra Buchanan-Hamilton (unpublished): Theobald (1876: 27; in part, includes “the Ganges, Bengal, the Irawadi, and the estuaries of the Indian and Malayan coasts” in the locality data). See also Wermuth and Mertens (1961: 247). Justified emendation of the original spelling. Illustration drawn 1804-5, # 522 India Office, London. Declared *nomen nudum* by Wermuth and Mertens (1961) since only published as a synonym, with no description, and not treated as an independent taxon before 1961 (ICZN Code). Type locality: specimens collected in India, Nepal and Burma were painted in Barrackpore, India (Archer, 1962: 39, 72); revised to “India: Ganges; Futtaghur” by Gray (1864:92), stated as quoted above in Theobald (1876: 27), later again revised to “Fatehgahr, Ganges” by Smith (1931: 162), accepted by Webb (1980: 72) and us as “Fategarh on the river Ganges, India.” Subjectively synonymized under *Trionyx indicus* Gray, 1831a:18, by Gray (1831b: 47). Inapp. syn. with “Irawadi” *Chitra*. [= *C. indica* (Gray, 1831a: 18)].

Gymnopus lineatus Duméril and Bibron, 1835: Theobald (1876: 27; in part, includes “the Ganges, Bengal, the Irawadi, and the estuaries of the Indian and Malayan coasts” in the locality data). See also Boulenger (1889: 264) and Wermuth and Mertens (1961: 247). Holotype: MNHN 6968. Type locality: originally “le Gange” river, India in Duméril and Bibron (1835); revised to “India: Ganges; Futtaghur” by Gray (1864:92); stated as quoted above in Theobald (1876). Conditionally and subjectively synonymized in Duméril & Bibron (1835: 492) with Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]), and *T. indicus* in Gray (1831b: 47). Subjectively synonymized with “*Trionyx Indicus*, Gray, *Syn. Rept.* 47” under *Chitra indica* (Gray, 1831a:18) by Gray (1844: 49). Inapp. syn. with “Irawadi” *Chitra*. [= *Chitra indica* (Gray, 1831a: 18)].

Gymnopus indicus (Gray, 1831a): Boulenger (1889: 263; in part, with “Ganges, Burma, Malay Peninsula, Borneo, Philippines” in locality data; synonym not italicized in original work; also see reference to Cantor (1847:10) which includes “*Pinang, Malayan Peninsula, (Estuaries, Sea Coast)*. Rivers in India, Philippine Islands” in locality data). Holotype (for synonym): RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]); but here used by Cantor (1847) is BMNH 1947.3.6.21, stuffed subadult, and BMNH 1947.3.6.22, skull from same specimen (see Boulenger 1889:263 cite same BMNH specimens as “a. Hgr. [half grown], stffd., skull separate. Pinang. Dr. Cantor. (Type.)”

under *P. cantoris* [= *P. cantorii* Gray, 1864: 90]. Type locality (for synonym): originally “India” in Gray (1831a); revised to “India: Ganges; Futtaghur” by Gray (1864:92), as quoted above in Boulenger (1889) and earlier by Cantor (1847), later again revised to “Fatehgahr, Ganges” by Smith (1931: 162), accepted by Webb (1980: 72) and us as “Fatehgahr on the river Ganges, India.” Cantor, unaware of the then undescribed genus *Pelochelys*, incorrectly synonymized his “*Pinang*” specimen with “*Chitra indica*, Gray: Catal.” (= Gray, 1844:49); see footnote in Cantor (1847:616): “In the living adult no is apparent, nor the outline of the costae, as represented in the figure [Plate 80] in *Illustrations of Indian Zoology*”. The synonym itself was objectively synonymized here with “*Chitra indica*, part., Gray, *Cat. Tort. P.* 49 (1844)”, and under “CHITRA INDICA. (Plate VI. fig. C. [thought to be a *P. cantorii* Gray, 1864: 90, with an erroneous *Chitra* pattern])” by Günther (1864: 50). Inapp. syn. with “Burma” *Chitra*. [= *C. indica* (Gray, 1831a: 18)].

Pelochelys cantorii Gray, 1864 [= *P. cantoris* in Boulenger (1889: 263)]: Boulenger (1889: 263; in part, due to synonymy here with “*Chitra indica*” (Gray, 1831a:18), “*Gymnopus indicus*” (Gray, 1831a:18) and “*Pelochelys bibronii*” (Owen, 1853: 185, 207); synonym not italicized in original work [see Theobald “Burma” specimens “b” and “c”, see also reference to Theobald (1876:28)]. Holotype: Jointly BMNH 1947.3.6.21, stuffed subadult, and BMNH 1947.3.6.22, skull from same specimen, listed here as “a. Hgr., stffd., skull separate. Pinang. Dr. Cantor. (Type.)”. Type locality: originally as “Malacca” (Malaysia) in Gray (1864:90); stated here as “Ganges, Burma, Malay Peninsula, Borneo, Philippines”; revised to “all other [excluding New Guinea] *Pelochelys* populations” by Webb (1995:308). Inapp. syn. with “Burma” *Chitra*; see Webb (1995: 308) for proper designation. [= *Pelochelys cantorii* Gray, 1864: 90].

Pelochelys cumingii Gray, 1864: Boulenger (1889: 263; in part, due to synonymy here with “*Chitra indica*” (Gray, 1831a:18), “*Gymnopus indicus*” (Gray, 1831a:18) and “*Pelochelys bibronii*” (Owen, 1853: 185, 207); synonym not italicized in original work). Holotype: none designated. Syntypes (see inapp. syn. with *C. indica* (Gray 1831a: 18), as “a” and “b” in Gray (1844: 49); see same specimens listed here as “f” and “g” and noted as “Types of *P. cumingii*”): BMNH 1947.3.4.5 and BMNH 1946.1. 22.13. Type locality: originally “Philippines” in Gray (1864: 90); stated here as “Ganges, Burma, Malay Peninsula, Borneo, Philippines” [but see reference to Gray (1864:90)]. Proper synonymy under *Pelochelys cantoris* [sic, = *P. cantorii* Gray, 1864:90], but inapp. syn. with “Burma” *Chitra* by Boulenger (1889: 263). Properly synonymized with *P. cantorii* Gray, 1864: 90, but inapp. syn. under *P. bibroni* (Owen, 1853: 185) by Smith (1931: 160), and Wermuth and Mertens (1961: 260). See proper subjective synonymy (“line priority”) under *Pelochelys cantorii* Gray, 1864: 90 by Webb (1995: 308). [= *Pelochelys cantorii* Gray, 1864: 90].

Pelochelys bibronii (Owen, 1853): Boulenger (1889: 263; in part, with “Ganges, Burma, Malay Peninsula, Borneo, Philippines” in locality data; synonym not italicized in original work). Incorrect subsequent spelling. Holotype: Jointly RCS (London) 954-959 and 1093-1094, a group of

skull and other skeletal parts from one specimen (see Webb, 1995: 301) – all lost in WW II. Neotype: AMS 3425, designated by Webb (1995: 302). Type locality: originally “Australian” [ex errore, in Owen (1853:185) and Gray (1864:90)]; as quoted above by Boulenger (1889), revised to “southern New Guinea” by Webb (1995: 302). Inapp. syn. with “Burma” *Chitra*. [= *Pelochelys bibroni* (Owen, 1853: 185, 207)].

Trionyx indicus Gray, 1831a: Boulenger (1889: 264; in part, with “Ganges and Irawaddy” as locality data; synonym not italicized in original work). See also Wermuth and Mertens (1961: 247). Justified emendation of original spelling. Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]). Type locality: originally “India” in Gray (1831a); “Ganges” on Plate 80, revised to “India: Ganges; Futtaghur” by Gray (1864:92), as quoted above by Boulenger (1889), later again revised to “Fatehgahr, Ganges” by Smith (1931: 162), accepted by Webb (1980: 72) and us as “Fatehgahr on the river Ganges, India.” Objectively synonymized here with “*Chitra indica*, part., Gray, *Cat. Tort. p.* 49 (1844).” Inapp. syn. with “Irawaddy” *Chitra*. [= *C. indica* (Gray, 1831a: 18)].

Trionyx aegyptiacus, var. *indicus* Gray, 1831a: Boulenger (1889: 264; in part, with “Ganges and Irawaddy” as locality data; synonym not italicized in original work). Justified emendation using lower case lettering, but incorrect subsequent spelling in reference here to Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]), incorrectly given as “1832” in Boulenger [1889: 264]. Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]). Type locality: originally “India” in Gray (1831a); stated as “Ganges” on Plate 80, revised to “India: Ganges; Futtaghur” by Gray (1864:92), as quoted above by Boulenger (1889: 264), later again revised to “Fatehgahr, Ganges” by Smith (1931: 162), accepted by Webb (1980: 72) and us as “Fatehgahr on the river Ganges, India.” Inapp. syn. as ssp. of *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, 1809: 12 (= *nomen substitutum* (Wermuth and Mertens, 1961: 282) for *Testudo triunguis* Forskål, 1775: 17), and with “Irawaddy” *Chitra*. Proper objective synonymy under *Trionyx indicus* Gray, 1831a:18 (see Webb, 1980: 62, 70) by Gray (1831b: 47). [= *Chitra indica* (Gray, 1831a: 18)].

Trionyx aegyptianus, var. *indicus* Gray, 1831a: Boulenger (1890:16; in part, includes “Ganges and Irawaddy” and Penang (Malaysia, through synonymy) in locality data; synonym not italicized in original work). Incorrect subsequent spelling. Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]). Type locality: originally “India” in Gray (1831a); stated as “Ganges” on Plate 80, revised to “India: Ganges; Futtaghur” by Gray (1864:92), as given above by Boulenger (1890:16), later again revised to “Fatehgahr, Ganges” by Smith (1931: 162), accepted by Webb (1980: 72) and us as “Fatehgahr on the river Ganges, India.” Inapp. syn. as ssp. of *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, 1809: 12 (= *nomen substitutum* (Wermuth and Mertens, 1961: 282) for *Testudo triunguis* Forskål, 1775:17), and with “Irawaddy” *Chitra*. Objective synonymy under

Trionyx indicus Gray, 1831a:18 (see Webb, 1980: 62, 70) by Gray (1831b: 47). [= *Chitra indica* (Gray, 1831a: 18)].

Trionyx (Gymnopus) Bibroni Owen, 1853: Pope (1935: 56; in part, includes “southern China and Burma southward through the Malay Archipelago to the Philippines and New Guinea.” and “Australia” in the locality data). Holotype: Jointly RCS (London) 954-959 and 1093-1094, a group of skull and other skeletal parts from one specimen (see Webb, 1995: 301) – all lost in WW II. Neotype: AMS 3425, designated by Webb (1995: 302). Type locality: originally “Australian” by Owen (1853:185); as quoted above by Pope (1935), later revised to “southern New Guinea” by Webb (1995: 302). Inapp. syn. with “Burma” *Chitra*. [= *Pelochelys bibroni* (Owen, 1853: 185, 207)].

Pelochelys poljakowii Strauch, 1890: Pope (1935: 56; in part, includes “southern China and Burma southward through the Malay Archipelago to the Philippines and New Guinea.” in the locality data). Species name correctly emended here to lower case. Holotype: none designated by Strauch (1890). Syntypes: Strauch (1890: 18) lists two skeletal specimens (#’s 7896 and 7897) in the Zool. Inst., Russian Acad. of Sci., St. Petersburg (= ZISP). Type locality: originally “Fu-tschau” [= Fuzhou, Fujian Prov., see Zhao and Adler (1993: 431)]. China by Strauch (1890: 18); as quoted above, but specifically as “Foochow” (China) by Pope (1935). Proper subjective synonymy under *P. cantorii* Gray, 1864:90, but inapp. syn. under *P. bibroni* (Owen, 1853:185), and with “Burma” *Chitra* by Pope (1935:56). [= *Pelochelys cantorii* Gray, 1864: 90].

Trionyx indica Gray, 1831a: Taylor (1970: 152, 153; in part, with “India, Burma, and the Malay Peninsula” in the locality data). Justified emendation of original spelling. Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]). Type locality: originally “India” in Gray (1831a); stated as “In India, fl. Ganges, Penang” in Gray (1831b), revised to “India: Ganges; Futtaghur” by Gray (1864: 92), revised again to “Fatehgahr, Ganges” by Smith (1931: 162), as “Fategharh, Ganges ‘Northern India’” and as quoted above in Taylor (1970: 152, 153), accepted by Webb (1980: 72) and us as “Fatehgahr on the river Ganges, India.” Proper objective synonymy with “Trionyx Indicus, Gray, *Syn. Rept.* 47” under *Chitra indica* (Gray, 1831a:18) by Gray (1844: 49). Inapp. syn. with “Burma” *Chitra*. [= *C. indica* (Gray, 1831a:18)].

Trionyx aegyptiacus var. *indica* Gray, 1831a: Taylor (1970: 152, 153; in part, with “India, Burma, and the Malay Peninsula” in the locality data). Justified emendation using lower case lettering in reference here to Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]). Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]). Type locality: originally “India” in Gray (1831a); stated as “Ganges” on Plate 80, revised to “India: Ganges; Futtaghur” by Gray (1864:92), revised again to “Fatehgahr, Ganges” by Smith (1931: 162), as “Fategharh, Ganges, India” and as quoted above in Taylor (1970: 152,153), accepted by Webb (1980: 72) and us as “Fatehgahr on the river Ganges, India.” Inapp. syn. as ssp. of *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, 1809: 12 (= *nomen substitutum* (Wermuth and Mertens,

1961: 282) for *Testudo triunguis* Forskål, 1775: 17), and with “Burma” *Chitra*. Proper objective synonymy under *Trionyx indicus* Gray, 1831a: 18 (see Webb, 1980: 62, 70) by Gray (1831b: 47). [= *Chitra indica* (Gray, 1831a: 18)].

***Chitra chitra chitra* Nutaphand 1990: comb. nov. [new combination].**

Trionyx Indicus Gray, 1831a: Gray (1831b: 47; in part, with “In India, fl. Ganges, Penang” in locality data). Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]). Type locality: originally “India” in Gray (1831a); as quoted above by Gray (1831b), as “Ganges” on Plate 80, revised to “India: Ganges; Futtaghur” by Gray (1864:92), later again revised to “Fatehgahr, Ganges” by Smith (1931: 162), accepted by Webb (1980: 72) and us as “Fatehgahr on the river Ganges, India.” Objectively synonymized as “Trionyx Indicus, Gray, *Syn. Rept.* 47” under *C. indica* (Gray, 1831a: 18) by Gray (1844: 49). Inapp. syn. with “Penang” (Malaysia) *Chitra*. [= *C. indica* (Gray, 1831a: 18)].

Trionyx Aegyptiacus, Var. [sic] *Indicus* Gray, 1831a: Gray (1831b: 47; in part, includes Ganges and Barrackpore, India and Penang, Malaysia in locality data). Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 [“1830-35”]). Type locality: originally “India” in Gray (1831a); as “In India, fl. Ganges, Penang” in Gray (1831b), as “Ganges” on Plate 80, revised to “India: Ganges; Futtaghur” by Gray (1864:92), later again revised to “Fatehgahr, Ganges” by Smith (1931: 162), accepted by Webb (1980: 72) and us as “Fatehgahr on the river Ganges, India.” Inapp. syn. as ssp. of *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, 1809: 12 (= *nomen substitutum* (Wermuth and Mertens, 1961: 282) for *Testudo triunguis* Forskål, 1775: 17), and with “Penang” (Malaysia) *Chitra*. Proper objective synonymy under *Trionyx indicus* Gray, 1831a: 18, by Gray (1831b: 47). [= *C. indica* (Gray, 1831a: 18)].

Testudo Chitra Buchanan-Hamilton (unpublished): Gray (1831b: 47; in part, includes Ganges and Barrackpore, India and Penang, Malaysia in locality data). Illustration drawn 1804-5, # 522 India Office, London. Declared *nomen nudum* by Wermuth and Mertens (1961) since only published as a synonym, with no description, and not treated as an independent taxon before 1961 (ICZN Code). Type locality: specimens collected in India, Nepal and Burma were painted in Barrackpore, India (Archer, 1962: 39, 72); revised to “India: Ganges; Futtaghur” by Gray (1864:92), later again revised to “Fatehgahr, Ganges” by Smith (1931: 162), accepted by Webb (1980: 72) and us as “Fatehgahr on the river Ganges, India.” Subjectively synonymized under *Trionyx indicus* Gray, 1831a:18, by Gray (1831b: 47). Inapp. syn. with “Penang” (Malaysia) *Chitra*. [= *C. indica* (Gray, 1831a: 18)].

Testudo membranacea Blumenbach, 1779: Gray (1831b: 47, referring to “Mus. Col. Surg.” specimen #1238.B; in part, includes Ganges and Barrackpore, India and Penang, Malaysia in locality data). *Nomen dubium* (available evidence is insufficient to permit recognition of the species to which this name was applied). Holotype: None designated. Type locality: “Guiana”, South America (= *ex errore*). Questionable synonymy under *Trionyx Aegyptiacus* Geoffroy

Saint-Hilaire, 1809:12, by Schweigger (1812: 366); *Trionyx indicus* Gray 1831a:18, by Gray (1831b: 47); and *Trionyx cartilaginea* (Boddaert, 1770) by Wermuth and Mertens (1961: 263). [= possibly *Amyda cartilaginea* (Boddaert, 1770: 1-39)].

Chitra indica (Gray, 1831a): Gray (1844: 49; in part, includes India, Philippine Islands, and Penang, Malaysia in locality data; synonym not italicized in original work). See also Cantor (1847: 616) and Günther (1864: 50). Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]). Type locality: originally "India" in Gray (1831a); stated as both "Philippine Islands" and "India" in Gray (1844: 49), revised to "India: Ganges; Futtaghur" by Gray (1864:92), later again revised to "Fatehgahr, Ganges" by Smith (1931: 162), accepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." Inapp. syn. with "Penang" (Malaysia) *Chitra*. [= *C. indica* (Gray, 1831a: 18)].

Trionyx Aegyptiacus, var. *Indicus* Gray, 1831a: Gray (1844: 49; in part, includes India, Philippine Islands, and Penang, Malaysia [by synonymy here with Gray, 1831b: 47] in locality data; synonym not italicized in original work here). Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]). Type locality: originally "India" in Gray (1831a), stated as "Ganges" on Plate 80, as both "Philippine Islands" and "India" in Gray (1844:49), revised to "India: Ganges; Futtaghur" by Gray (1864:92), again revised to "Fatehgahr, Ganges" by Smith (1931: 162), accepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." Inapp. syn. as ssp. of *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, 1809: 12 (= *nomen substitutum* (Wermuth and Mertens, 1961: 282) for *Testudo triunguis* Forskål, 1775: 17), and with "Penang" (Malaysia) *Chitra*. Objective synonymy under *Trionyx indicus* Gray 1831a:18 (see Webb, 1980: 62, 70), by Gray (1831b: 47). [= *Chitra indica* (Gray, 1831a: 18)].

Gymnopus indicus (Gray, 1831a): Cantor (1847: 10, 616; in part, includes "Pinang, Malayan Peninsula, (Estuaries, Sea Coast). Rivers in India, Philippine Islands" in locality data; synonym not italicized in original work). Holotype (for synonymy): RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]); but here used by Cantor (1847) is BMNH 1947.3.6.21, stuffed subadult, and BMNH 1947.3.6.22, skull from same specimen (see Boulenger 1889:263 cite same BMNH specimens as "a. Hgr. [half grown], stffd., skull separate. Pinang. Dr. Cantor. (Type.)" under *P. cantoris* [= *P. cantorii* Gray, 1864: 90]). Type locality (for synonymy): originally "India" in Gray (1831a); stated as quoted above in Cantor (1847), revised to "India: Ganges; Futtaghur" by Gray (1864:92), later again revised to "Fatehgahr, Ganges" by Smith (1931: 162), accepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." Cantor, unaware of the then, undescribed genus *Pelochelys*, incorrectly synonymized his "Pinang" specimen with "Chitra indica, Gray: Catal." (= Gray, 1844:49); see footnote in Cantor (1847:616): "In the living adult no is apparent, nor the outline of the costae, as represented in the figure [Plate 80] in *Illustrations of Indian Zoology*". The synonym itself was objectively synonymized under "CHITRA INDICA. (Plate VI.

fig. C. [thought to be a *P. cantorii* Gray, 1864: 90, with an erroneous *Chitra* pattern])" by Günther (1864: 50). Inapp. syn. with "Pinang, Malayan Peninsula" *Chitra*. [= *C. indica* (Gray, 1831a: 18)].

Pelochelys cantorii Gray, 1864: 90; in part, due to synonymy here with "*Chitra indica*" (Gray, 1831a: 18) and "*Gymnopus indicus*" (Gray, 1831a: 18); synonym not italicized in original work. Holotype: Jointly BMNH 1947.3.6.21, stuffed subadult, and BMNH 1947.3.6.22, skull (see Figs. 9 and 10) from same specimen (see reference here to Cantor (1847) specimen); also see Boulenger's (1889:263) [Cantor (1847)] specimen "a" as "Type". Type locality: here as "Malacca" (Malaysia); includes India, Penang, Malaysia and Philippines in locality data through synonymy; revised to "all other [excluding New Guinea] *Pelochelys* populations" by Webb (1995:308). Inapp. syn. with "Penang, Malaysia" *Chitra*; see Webb (1995: 308) for proper designation. [= *Pelochelys cantorii* Gray, 1864: 90].

Pelochelys cumingii Gray, 1864: 90; in part, due to synonymy here with "*Chitra indica*" (Gray, 1831a: 18); synonym not italicized in original work. Note incorrect subsequent spelling (*P. cumingii*) in Smith (1931: 160). Holotype: none designated. Syntypes (see inapp. syn. with *C. indica* (Gray 1831a: 18), as "a" and "b" in Gray (1844: 49); see also same specimens "f" and "g" designated by Boulenger (1889: 263) as "Types of *P. cumingii*"): BMNH 1947.3.4.5 and BMNH 1946.1. 22.13. Type locality: here as "Philippines"; includes India, Penang, Malaysia and Philippines in locality data through synonymy. Inapp. syn. with "Penang" [Malaysian, by synonymy with Gray (1831b: 47) through reference to Gray (1855: 70)] *Chitra*, by Gray (1864: 90). Proper synonymy under *Pelochelys cantoris* [sic] Gray, 1864:90, but inapp. syn. with "Malay Peninsula" *Chitra* by Boulenger (1889: 263). Properly synonymized with *P. cantorii* Gray, 1864: 90, but inapp. syn. under *P. bibroni* (Owen, 1853:185), by Smith (1931: 160), and Wermuth and Mertens (1961: 260). See proper subjective synonymy ("line priority") under *Pelochelys cantorii* Gray, 1864: 90 by Webb (1995: 308). [= *Pelochelys cantorii* Gray, 1864: 90].

Chitra Indica var. [sic] *Cumingii* (Gray, 1864): Boettger (1886: 93; in part, includes India, Nepal, Penang, Malaysia and Philippines in locality data). Holotype: none designated. Syntypes (see inapp. syn. with *C. indica* (Gray 1831a: 18), as "a" and "b" in Gray (1844: 49); see also same specimens "f" and "g" designated by Boulenger (1889: 263) as "Types of *P. cumingii*"): BMNH 1947.3.4.5 and BMNH 1946. 1. 22.13. Type locality: originally "Philippinen" in Gray (1864: 90). Inapp. syn. here as ssp. of *C. indica* (Gray, 1831a: 18), and with "Penang" [Malaysia, see references lead to Gray (1831b: 47)] *Chitra*. Proper synonymy under *P. cantoris* [sic] Gray, 1864: 90, but inapp. syn. with "Penang" and "Pinang" [Malaysia, see references to Gray (1831b:47) and Cantor (1847:10)] *Chitra*, by Boulenger (1889: 263). Proper subjective synonymy ("line priority") under *P. cantorii* Gray, 1864: 90 by Webb (1995: 308). [= *Pelochelys cantorii* Gray, 1864: 90].

Pelochelys cantoris [sic] Gray, 1864: Boulenger (1889: 263; in part, due to synonymy here with "Chitra indica" (Gray, 1831a:18), "Gymnopus indicus" (Gray, 1831a:18) and "Pelochelys bibronii" (Owen, 1853: 185, 207); synonym not italicized in original work). Holotype: Jointly BMNH

1947.3.6.21, stuffed subadult, and BMNH 1947.3.6.22, skull from the same specimen (here as Cantor's specimen "a" identified as the "Type"). Type locality: originally "Malacca" in Gray (1864: 90); stated here as "Ganges, Burma, Malay Peninsula, Borneo, Philippines"; revised to "all other [excluding New Guinea] *Pelochelys* populations" by Webb (1995:308). Declared "an unjustified emendation" of *P. cantorii* Gray, 1864: 90 by Webb (1995: 308), and an incorrect subsequent spelling by us. Inapp. syn. with "Malay Peninsula" *Chitra*. [= *Pelochelys cantorii* Gray, 1864: 90].

Pelochelys bibronii (Owen, 1853): Boulenger (1889: 263; in part, includes "Ganges, Burma, Malay Peninsula, Borneo, Philippines" in locality data; synonym not italicized in original work). Incorrect subsequent spelling. Holotype: Jointly RCS (London) 954-959 and 1093-1094, a group of skull and other skeletal parts from one specimen (see Webb, 1995: 301) – all lost in WW II. Neotype: AMS 3425, designated by Webb (1995: 302). Type locality: originally "Australian" [*ex errore*, by Owen (1853:185) and Gray (1864:90)], as quoted above by Boulenger (1889), revised to "southern New Guinea" by Webb (1995: 302). Inapp. syn. with "Malay Peninsula" *Chitra*. [= *Pelochelys bibronii* (Owen, 1853: 185, 207)].

Trionyx aegyptianus, var. *indicus* Gray, 1831a: Boulenger (1890:16; in part, includes "Ganges and Irrawaddy" and Penang (Malaysia, through synonymy) in locality data; synonym not italicized in original work). Incorrect subsequent spelling. Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]). Type locality: originally "India" in Gray (1831a); "Ganges" on Plate 80, revised to "India: Ganges; Futtaghur" by Gray (1864: 92), as given above by Boulenger (1890:16), later again revised to "Fatehgahr, Ganges" by Smith (1931: 162), accepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." Inapp. syn. as ssp. of *Trionyx Aegyptiacus* Geoffroy Saint-Hilaire, 1809: 12 (= *nomen substitutum* (Wermuth and Mertens, 1961: 282) for *Testudo triunguis* Forskål, 1775:17), and with "Penang" (Malaysia) *Chitra*. Objective synonymy under *Trionyx indicus* Gray, 1831a:18 (see Webb, 1980: 62, 70) by Gray (1831b: 47). [= *Chitra indica* (Gray, 1831a: 18)].

Pelochelys bibronii (Owen, 1853): Smith (1931: 160, 161; in part, includes "? Bengal; the Indo-Chinese Peninsula and Southern China; Hainan; ? the Malay Peninsula; Sumatra; Borneo; the Philippine Islands; New Guinea" in the locality data; synonym not italicized in original work; see also reference to "Australia" [*ex errore*, by Owen (1853) and Gray (1864)], under *Trionyx (Gymnopus) bibronii* Owen, 1853: 185). Holotype: Jointly RCS (London) 954-959 and 1093-1094, a group of skull and other skeletal parts from one specimen (see Webb, 1995: 301) – all lost in WW II. Neotype: AMS 3425, designated by Webb (1995: 302). Type locality: originally "Australian" (see above) by Owen (1853:185); as quoted above by Smith (1931: 161), later revised to "southern New Guinea" by Webb (1995: 302). Inapp. syn. with "Malay Peninsula" *Chitra*. See Smith (1931: 161) mention "Cantor's type [presently *P. cantorii* Gray, 1864: 90, but here considered *P. bibronii* (Owen, 1853: 185)

by Smith (1931)], said to have come from Malacca, is the only known example from the Malay Peninsula." [= *Pelochelys bibronii* (Owen, 1853: 185, 207)].

Pelochelys poljakowii Strauch, 1890: Smith (1931: 160, 161; in part, includes "? Bengal; the Indo-Chinese Peninsula and Southern China; Hainan; ? the Malay Peninsula; Sumatra; Borneo; the Philippine Islands; New Guinea" in the locality data). Species name correctly emended here to lower case. Holotype: none designated by Strauch (1890). Syntypes: Strauch (1890: 18) lists two skeletal specimens (#'s 7896 and 7897) in the Zool. Inst., Russian Acad. of Sci., St. Petersburg (= ZISP). Type locality: "Fu-tschau" [= Fuzhou, Fujian Prov., see Zhao and Adler (1993: 431)], China by Strauch (1890); as quoted above by Smith (1931:161). Proper subjective synonymy with *P. cantorii* Gray, 1864:90, but inapp. syn. with "Malay Peninsula" *Chitra* by Smith (1931: 160). [= *Pelochelys cantorii* Gray, 1864: 90].

Trionyx indica Gray, 1831: Taylor (1970: 152; in part, gives "Fategarh, Ganges 'Northern India'", but through synonymy also Penang, Malaysia and Philippines included in locality data). Holotype: RCS (London) #1238.B – lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]). Type locality: originally "India" in Gray (1831a); "Ganges" on Plate 80, revised to "India: Ganges; Futtaghur" by Gray (1864:92), later again revised to "Fatehgahr, Ganges" by Smith (1931: 162), as quoted above by Taylor (1970), accepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." Proper objective synonymy with "Trionyx Indicus, Gray, *Syn. Rept.* 47" under *Chitra indica* (Gray, 1831a:18) by Gray (1844: 49). Inapp. syn. with "Penang" (Malaysia) *Chitra*. [= *C. indica* (Gray, 1831a: 18)].

Chitra chitra Nutaphand, 1990: 103. Holotype: none stated, but herein designated as the specimen illustrated on page 104 of the original description, by us. Type locality: none stated, but restricted to "Kanburi (presently Kanchanaburi), where the Khwae Noi and the Khwae Yai rivers join to form the Mae Klong River in Kanchanaburi Province, Thailand", by us [= *Chitra chitra chitra* Nutaphand, 1990: 103].

***Chitra chitra javanensis* ssp. nov.**

Chitra indica (Gray, 1831a): Müller (1923: 54; in part, having India, Philippine Islands, Penang, Malaysia and "Buitenzorg, Java" in the locality data). See Smith (1931:160) for "Sumatra" locality. Holotype: RCS (London) #1238.B - lost. Neotype: specimen illustrated on Plate 80 in *Illus. Ind. Zool.* (Gray, 1831 ["1830-35"]). Type locality: originally "India" in Gray (1831a), "Ganges" on Plate 80, revised to "India: Ganges; Futtaghur" by Gray (1864:92), as given above by Müller (1923), later again revised to "Fatehgahr, Ganges" by Smith (1931: 162), accepted by Webb (1980: 72) and us as "Fatehgahr on the river Ganges, India." Inapp. syn. with "Java" and "Sumatra" *Chitra*. [= *C. indica* (Gray, 1831a: 18)].

Pelochelys bibronii (Owen, 1853): Smith (1931: 160, 161; in part, includes "? Bengal; the Indo-Chinese Peninsula and Southern China; Hainan; ? the Malay Peninsula; Sumatra; Borneo; the Philippine Islands; New Guinea" in the locality

data; synonym not italicized in original work; see also reference to “Australia” [*ex errore*, by Owen (1853) and Gray (1864)], under *Trionyx (Gymnopus) bibroni* Owen, 1853: 185). Holotype: Jointly RCS (London) 954-959 and 1093-1094, a group of skull and other skeletal parts from one specimen (see Webb, 1995: 301) – all lost in WW II. Neotype: AMS 3425, designated by Webb (1995: 302). Type locality: originally “Australian” (see above) by Owen (1853:185); as quoted above by Smith (1931: 161), later revised to “southern New Guinea” by Webb (1995: 302). Inapp. syn. with “Sumatra” *Chitra*. [= *Pelochelys bibroni* (Owen, 1853: 185, 207)].

Pelochelys poljakowii Strauch, 1890: Smith (1931: 160, 161; in part, includes “? Bengal; the Indo-Chinese Peninsula and Southern China [specifically “type loc. Fuchow, China”]; Hainan; ? the Malay Peninsula; Sumatra; Borneo; the Philippine Islands; New Guinea” in the locality data). Species name correctly emended here to lower case. Holotype: none designated by Strauch (1890). Syntypes: Strauch (1890: 18) lists two skeletal specimens (#’s 7896 and 7897) in the Zool. Inst., Russian Acad. of Sci., St. Petersburg (= ZISP). Type locality: “Fu-tschau” [= Fuzhou, Fujian Prov., see Zhao and Adler (1993: 431)], China by Strauch (1890); as quoted above by Smith (1931: 161). Proper subjective synonymy with *P. cantorii* Gray, 1864:90, but inapp. syn. with “Sumatra” *Chitra* by Smith (1931: 160). [= *Pelochelys cantorii* Gray, 1864: 90].

Pelochelys cantorii Gray, 1864: Smith (1931: 160, 161; in part, includes “? Bengal; the Indo-Chinese Peninsula and Southern China; Hainan; ? the Malay Peninsula; Sumatra; Borneo; the Philippine Islands; New Guinea” in the locality data). Holotype: Jointly BMNH 1947.3.6.21, stuffed subadult, and BMNH 1947.3.6.22, skull from same specimen; see reference here to Cantor (1847) specimen in Gray (1864:90); also see Boulenger’s (1889:263) [Cantor (1847)] specimen “a” as “Type”. Type locality: originally “Malacca” (Malaysia) by Gray (1864:90); as quoted above by Smith (1931:161); revised to “all other [excluding New Guinea] *Pelochelys* populations” by Webb (1995: 308). Inapp. syn. with “Sumatra” *Chitra*. See Webb (1995: 308) for proper designation. [= *Pelochelys cantorii* Gray, 1864: 90].

Pelochelys cummingii Gray, 1864: Smith (1931: 160, 161; in part, includes “? Bengal; the Indo-Chinese Peninsula and Southern China; Hainan; ? the Malay Peninsula; Sumatra; Borneo; the Philippine Islands; New Guinea” in the locality data). Incorrect subsequent spelling. Holotype: none designated. Syntypes (see inapp. syn. with *C. indica* (Gray 1831a: 18), as “a” and “b” in Gray (1844: 49); see also same specimens “f” and “g” designated by Boulenger (1889: 263) as “Types of *P. cummingii*”): BMNH 1947.3.4.5 and BMNH 1946.1. 22.13. Type locality: originally “Philippines” by Gray (1864: 90); Smith (1931:160) cites Gray (1864:90) as “type loc. Philippine Is.”; and as quoted above by Smith (1931: 161). Proper subjective synonymy with *P. cantorii* Gray, 1864: 90, but inapp. syn. with “Sumatra” *Chitra* by Smith (1931: 160, 161). See proper subjective synonymy (“line priority”) under *Pelochelys cantorii* Gray, 1864: 90 by Webb (1995: 308). [= *Pelochelys cantorii* Gray, 1864: 90].

Chitra chitra Nutaphand, 1990: Iskandar (2000: 82; in part [synonym here refers to nominate subspecies], giving “South Thailand, Peninsular Malaysia, Sumatra and Java” in the locality data). See also Samedi and Iskandar (2000: 106). Holotype: none stated, but herein designated as the specimen illustrated on page 104 of the original description, by us. Type locality: none stated by Nutaphand (1990: 103), but restricted to “Kanburi (presently Kanchanaburi), where the Khwae Noi and the Khwae Yai rivers join to form the Mae Klong River in Kanchanaburi Province, Thailand”, by us. Proper synonymy prior to *Chitra chitra javanensis* ssp. nov. described herein. Presently inapp. syn. (synonym herein *C. c. chitra*) with “Sumatra and Java” *Chitra*. [= *Chitra chitra chitra* Nutaphand, 1990: 103].

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NOTES ADDED IN PROOF

Jaekel (1911) described two new fossil *Chitra* species from the Trinil formations (approximately one million years old) of eastern Java. He based his new species *Chitra minor* upon a single xiphiplastron and associated hypoplastron, and his *Chitra Selenkae* [sic] upon a large adult carapace, two entoplastra, a xiphiplastron, and various other bones. Although Jaekel himself (1911: 81) concluded that his two fossil *Chitra* species were not conspecific with any living *Chitra* species, because these taxa were named much earlier than either Nutaphand’s *Chitra chitra* or our new living subspecies of *C. chitra* from Java, they need to be discussed. An examination of the Jaekel material and discussion in the light of the ICZN Rules is thus presented.

The two plastral bones attributed to *Chitra minor*, in our opinion, are not correctly assigned to the genus *Chitra*. Jaekel himself noted various points for which the material differed from typical *Chitra*, including the relatively small size in combination with the robust callosities typical of a fully adult turtle; the very small protrusions from the xiphiplastron; and the much deeper inward curvature of the inguinal notch. Comparison of Jaekel’s illustrations with actual skeletal specimens of *Chitra chitra*, *Chitra indica*, and other trionychids in the Chelonian Research Institute collection indicates beyond reasonable doubt that they are attributable to *Pelochelys*, not to any species of *Chitra*. Both bones are broken off on the left side (i.e., the right side of the living animal), with loss of some diagnostic areas; but the inguinal incurving is much deeper than in *Chitra* although appropriate for *Pelochelys*, and in *Chitra* the hyo-hypoplastral suture on each side is transverse for most of its length but strongly curved posteriorly in its distal section. In the Jaekel specimen the suture is straight for at least the entire width of the specimen as preserved, showing no such posterior redirection. Furthermore, in younger *Chitra* specimens there is a large, circular fontanelle in the posterior part of the line of contact between the xiphiplastra, and even in very old, large specimens the fontanelle is still present although somewhat narrower. In the Jaekel specimen there is no trace of this fontanelle, and only a

few minor projections are present on the midline and anterior margins of the bone. All of these features are characteristic of *Pelochelys*. We propose that *Chitra minor* be considered a junior synonym of the extant form of *Pelochelys* on the island of Java; i.e., *P. cantorii*.

The other Jaekel species (*C. Selenkae*) presents many typical *Chitra* characteristics, including a series of neural bones that separate all pleural bone pairs except for the posterior part of the eighth pair, and a xiphiplastron showing evidence of a large fontanelle in the posterior part of the midline xiphiplastral junction. Also present is a strong anterolateral xiphiplastral prong adjacent to a deep notch and a second, much shorter prong; this is typical of *Chitra* whereas in *Pelochelys* the outer prong is much less developed. The interdigitations along both the anterior and the midline edges of the bone are well developed, as in typical *Chitra* and contrasting with the condition in *Pelochelys*.

The carapace of *C. Selenkae* is shown inverted in Jaekel's illustration (Fig. 1, Plate XV), but is essentially complete, although the rib tips are either missing or covered by the outer edges of the pleural bones [not normal for *Chitra*, but possible in this very large (64 cm midline length) specimen]. Overall, the carapace is less rounded than the typical bony carapace of *Chitra indica* or *C. chitra*, which are nearly circular, but not dissimilar to an even larger fossil *Chitra* carapace examined in central Java by PCHP in 1997. This is illustrated in Pritchard (2001, fig. 2), and has a maximum CL of 738 mm and midline CL of 702 mm. The two largest museum specimens of contemporary *Chitra chitra* are in the collection of Chulalongkorn University (Bangkok) and both measure 610 mm. An assumption at the time of inspection of the 738 mm specimen was that it was possibly a cast or a "man-made" gigantic contemporary specimen rather than a real fossil; but our subsequent reading of the Jaekel paper lends support to the likelihood that it is genuine, and a further example of *Chitra Selenkae*.

Although we find scant morphological justification for recognizing the fossil *Chitra Selenkae* and the living *Chitra chitra* as different species, we do not propose nomenclatural changes for the extant species on the grounds of chronological priority, for several reasons.

Paleontology and neontology are "different worlds", with such different techniques that comparisons are difficult or even impractical. Modern *Chitra* species are differentiated primarily by genetic divergence, coloration, pattern, and su-

perfluous features such as forelimb lamellae and pseudodigits. Such characters are not an option for fossils, which have to be based upon whatever is available, often a few skeletal fragments. There exists the possibility of different chronologically "vertical" phases of a single lineage (allochronic or chronospecies).

Because Jaekel's *Chitra Selenkae* was described long before Nutaphand's proposal of *Chitra chitra*, strict priority consideration would affect the nomenclature, not only of the contemporary *Chitra* taxon in Java, but of *Chitra chitra* as a whole (i.e. in Thailand and Malaysia as well as Indonesia). Such changes to current or popular usage based entirely upon discovery of an unused senior synonym are strongly discouraged by the latest edition of the Rules of Nomenclature (see Article 23 etc., ICZN 1999).

Similar, yet different precedents where the fossil name was retained or resurrected were less taxonomically destabilizing than potentially seen here. In the case of *Elseya lavarackorum* (Gaffney et al., 1989) the subsequently discovered living form had not received a new name at the time they were recognized as conspecific with the fossil form. Iverson's (1979) synonymy of *Kinosternon flavescens stejnegeri* Hartweg, 1938 under *Kinosternon flavescens arizonense* Gilmore, 1922, involved what was then thought to be only subspecific forms from the same restricted locality, not affecting the taxonomic stability of the entire *Kinosternon flavescens* (Agassiz, 1857) species "complex". A precedent more directly comparable was the naming of *Pseudemys nelsoni* by Carr (1938), and the retention of this name by all modern authors despite the demonstration by Jackson (1978) that the fossil forms *Trachemys jarmani* and *Deirochelys floridana*, both of Hay (1908), were actually conspecific with *P. nelsoni*.

As first reviewer, for the sake of taxonomic stability, the reasons above, and with the knowledge that Jaekel's *Chitra Selenkae* is a name not used since its original description 91 years ago, therefore effectively "lost" to science for that period of time, we will proceed here to recognize the extant Java *Chitra* as a subspecies of Nutaphand's (1990) *Chitra chitra*, and we will agree with Jaekel (1911) that his *Chitra selenkae* is not conspecific with any Recent form of Java *Chitra*. If ever, Jaekel's *Chitra selenkae* can be confirmed as conspecific with the living form of *Chitra* found on Java, as first reviewer, we propose it be designated as a junior synonym of Nutaphand's (1990) *Chitra chitra*.