Japanese Journal of Herpetology 14(3): 143–159., June 1992

Taxonomic Re-evaluation of the Two Subspecies of *Geoemyda spengleri spengleri* (Gmelin, 1789) (Reptilia: Emydidae)

YUICHIROU YASUKAWA, HIDETOSHI OTA, AND TSUTOMU HIKIDA

Abstract: Detailed comparisons are made between *Geoemyda spengleri spengleri* and *G. s. japonica* for the first time on the basis of large samples. There are considerable differences between these subspecies, which suggest that both forms should be more appropriately treated as independent species. On the other hand, results of comparisons with other closely related species indicate that *G. spengleri* and *G. japonica* compose a monophyletic group.

Key words: Taxonomy; *Geoemyda japonica*; *Geoemyda spengleri*; Batagurinae; Ryukyu Archipelago

The black breasted leaf turtle, *Geoemyda spengleri*, was first reported without assignment of a definite name by Walbaum (1785), and then was described as *Testudo spengleri* by Gmelin (1789) on the basis of Walbaum's specimen, probably brought from the East Indies (Pope, 1935). The species has since been reported from southeastern China (Kwangtung, Kwangsi and Hainan Is.), eastern Indochina (Vietnam, Laos and Cambodia), Indo-Australian Archipelago (Batu Islands, Sumatra and Borneo), Philippines, and the Ryukyu Archipelago of Japan (Okinawajima Is., Kumejima Is., and Tokashikijima Is.) (Rooij, 1915; Wermuth and Mertens, 1977; Toyama, 1985; Iverson, 1986, 1992; Tian et al., 1986). However, records from the Indo-Australian Archipelago and the Philippines have derived only from very old literature descriptions (Strauch, 1865; Elera, 1895), and no verifications have been made subsequently. Thus, *G. spengleri* is considered to be extralimital in these regions (Taylor 1920; Iverson, 1986, 1992).

The holotype of *G. spengleri* was described as lacking axillary and inguinal scutes. Relative lengths of midseams of its plastral shields (plastral formula) can be formulated as abdominal > humeral = pectoral = femoral > anal > gular (Walbaum, 1785). Boulenger (1889) noted that the Chinese ones also lack axillary and inguinal, but that their plastral formula is abdominal > femoral > pectoral > humeral > anal > gular. Stejneger (1907) first recorded the species from Japan, and stated that Japanese specimens can be discriminated from Chinese ones described by Boulenger (1889) in having a pair of prominent axillaries and a different plastral formula. Fang (1930) compared the specimens from Kwangsi, China, with those described by Stejneger (1907), and noted that the former differs from the latter in the shape of the cervical, presence of more distinct carapace serration, and absence of spines at the base of the tail. Based on Stejneger's (1907) accounts, Fan (1931) recognized two subspecies with assumption of their distributions as follows: *G. spengleri sinensis* from the continent, and *G. s. japonica* from Japan and other Pacific islands. He, however, did not refer to the nominotypical form. Furthermore, the range of the latter form he listed is actually incorrect (see above). Fang (1934) argued that the plastral formula is highly variable within a population, and that the presence of the axillary is probably accidental. He thus suspected that the two subspecies are not separable from each other in reality. These authors, however, did not compare the two forms directly. Pope (1935), after comparing six specimens from the continent and four from the Ryukyus, followed Fan (1931) and considered that the presence or absence of the axillary is a valid discriminant character for the two forms. With the assumption that Gmelin's (1789) specimen represents the continental form, he defined the subspecies as follows: *G. s. japonica* from the Ryukyus, characterized by the prominent axillary and occasional trace of the inguinal, and *G. s. spengleri* from the continent, characterized by the absence of the axillary and inguinal. He further predicted that each of these two forms would be accorded the status of full species after detailed studies are made.

Accepted 22 May 1992

However, no subsequent systematic studies have ever been carried out, probably due to the difficulties of access to the large samples necessary for detailed analyses. Only recently, Chinese and Vietnamese *G. spengleri* have become available through pet dealers, and we have compared the two forms morphologically using such imported animals as well as museum and zoo specimens. The comparisons have revealed that there is a large number of characters in which *G. s. spengleri* and *G. s. japonica* distinctly differ from each other. These results suggest that both forms should be more appropriately treated as independent species.

Materials and Methods

A total of 49 specimens of *G. s. spengleri* from the Asian continent (26 males and 23 females) and 50 specimens of *G. s. japonica* from the Ryukyu Archipelago (21 males, 22 females, 2 juveniles and 4 adults of unknown sex) were examined (see "Specimens examined" for further details). Of the former, only one specimen bore detailed locality data; localities of the others were not detectable in detail. However, since all these showed no apparent morphological differences with each other, we adopted an a priori assumption of their monophyly, and treated the continental specimens as a single operational taxonomic unit collectively.

Most specimens were sexed on the basis of the length and thickness of the tail, since males have distinctly longer and thicker tails than females (Ernst and Barbour, 1989; Pritchard, 1979). Two juveniles were not sexed, because they did not show any sexual difference. Four specimens represented only by shells were not sexed, either.

Colors were recorded from living turtles and color transparencies, using a set of 500 color cards (Fukuda, 1965). For skeletal characters, we examined four skulls and mandibles and two sets of postcranial skeletons of *G. s. spengleri*, and three skulls and mandibles and two sets of postcranial skeletons of *G. s. japonica*.

Straight line measurements were made to the nearest 0.1 mm for the following characters using dial or slide calipers: greatest carapace (CL1) and plastron lengths (PL1), midline carapace (CL2) and plastron lengths (PL2), greatest width of carapace (CW), shell depths at seams between vertebrals 1 and 2 (SD1-2), 2 and 3 (SD2-3) and 4 and 5 (SD4-5) (SD1-2 is only slightly smaller than the greatest shell depth), bridge lengths at its contact with marginals (DBL) and at its shortest dimension (VBL), width of anterior (APW) and posterior (PPW) plastral lobes at bridge level, greatest head width (HW), distance between centers of nostrils (INL), tail length from posterior notch of plastron to tail tip (TL), distance from posterior end of vent to tail tip (VTL), greatest length (CEL) and width of cervical (CEW), greatest widths of vertebrals 3 (V3W), 4 (V4W) and 5 (V5W), greatest length of vertebral 5 (V5L), length of vertebral 5 from its anterior margin to the widest position (V5Lm), lengths of pleurals 2 (P2L) and 3 along lateral keel (P3L), greatest lengths of gulars (GL) and anals (AnL), length of seam between marginals 12 (M12L), and length of seam between pleurals 4 and vertebral 5 (P4W). Midseam lengths between gulars (G), humerals (H), pectorals (P), abdominals (Ab), femorals (F) and anals (An) were measured, and plastral formulae were determined following the method proposed by Lovich and Ernst (1989).

Sexual and intersubspecific differences in adult CL2 were examined using Mann-Whitney's U test. All the other measurements of adult specimens were compared as log-transformed functions of CL2 using the Statistical Analysis System (SAS: SAS, 1985). Significance levels for all analyses were set at 0.05. In consideration of sexual dimorphism, each morphometric character was first compared between the sexes within each subspecies. When one or both of the two subspecies showed significant sexual differences in a given measurement, the character was compared between the subspecies separately in males and females. In both sexual and intersubspecific analyses, homogeneities in slopes of regression lines were satisfied for all measurements in which correlations with CL2 were statistically significant. Those measurements were therefore compared using analysis-of-covariance (ANCOVA) procedure. Probably due to the small sample size and large variation, the following measurements showed no significant correlations with CL2: INL, TL, VTL, CEW, V3W, GL, M12L, and P in male *G. s. spengleri*, INL, GL, M12L, G, and H in female *G. s. spengleri*, INL in adult *G. s. spengleri*, and TL, VTL, CEL, CEW, GL, G, and An in female *G. s. japonica*. Assuming that these measurements essentially correlate with CL2 and satisfy the slope homogeneity presumption, we analyzed all but INL, TL, and VTL by the same method as above. Since INL is considered to correlate more strongly with head size than with shell size, this value was compared in relation to HW between *G. s. spengleri* and *G. s. japonica* by ANCOVA procedure. Degree of tail tip wear is highly variable among individuals in both subspecies, and it makes correlation of TL and VTL against CL2 weaker.

Specimens Examined

In the following sections, catalogue numbers of specimens deposited in herpetological collections of the Department of Zoology, Kyoto University, Teikyo University of Technology, and personal collections of R. Hirayama, A. Kamata, R. Aoki, and the senior author are preceded by KUZ, TUT, RH, AK, RA and YY, respectively. The other acronyms are those suggested by Leviton et al. (1985).

G. s. spengleri. China: Kwangsi: Loshiang-Kutchen: USNM 84992; China or adjacent region: KUZ 9994, 12630, 19399–19407, TUT b15, RH 847, 856, 857, 864–867, AK 88.1.20., 90.7.7.1, 90.7.7.2, 90.6.30.1–90.6.30.4, RA 1–17 (live), YY 1-5 (live).

G. s. japonica. Ryukyu Archipelago: Okinawajima Is.: NSMT 02083-02086, OMNH R3334, two unnumbered specimens of OPM, USNM 34053, 55715, 123031, 123314–123319; Ryukyu Archipelago: Kumejima Is.: KUZ 19408, OMNH R3333, four live specimens released after being examined; localities unknown: KUZ 19409-19412, RH 480–482, 19 live animals kept in Zoo Okinawa, one live animal kept in Himeji City Aquarium,one live animal kept by M. Toyama.

Species Recognized

Geoemyda spengleri (Gmelin)

Testudo spengleri Gmelin, 1789 : 1034.
Testudo serpentina Latreille, 1802 : 163 (nec Linnaeus, 1758).
Testudo serrata Shaw, 1802 : 51.
Testudo tricarinata Bory de St. Vincent, 1804 : 308 (nec Schoepff, 1792).
Emys spengleri Schweigger, 1814 : 41.
Geoemyda spengleri Gray, 1834 : 99; Siebenrock, 1907 : 1760; 1909 : 495; Rooij, 1915 : 298; Fang, 1930 : 118, 121 (part); 1934 : 174, 175 (part); Smith, 1931 : 90.
Nicoria spengleri Gray, 1855 : 17; Boulenger, 1889 : 120; Siebenrock, 1906 : 583.
Clemmys spengleri Strauch, 1862 : 32; 1865 : 63.
Geoemyda spengleri sinensis Fan, 1931 : 146.
Geoemyda spengleri spengleri Pope, 1934 : 2; 1935 : 35; Bourret, 1941 : 155; Wermuth and Mertens, 1977 : 33; Ernst and Barbour, 1989 : 155; Iverson, 1992 : 123.

Holotype.—Not located, locality unknown (presumably from the East Indies: Pope, 1935).

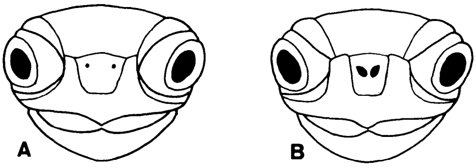

FIG. 1. Frontal view of head of *Geoemyda spengleri* (A), and *G. japonica* (B).

Diagnosis.—Small species of the Batagurinae $74.1 \leqq \mathrm{CL1} \leqq 113.4$ mm, $67.4 \leqq \mathrm{CL2} \leqq 107.1$ mm in adult; mostly without axillary (48/49) and inguinal scutes (48/49); anterior and posterior margins of carapace serrated; plastron hingeless, notched anteriorly and posteriorly; midseam between femorals longer than that between anals; plastron blackish, with light colored margin; snout not projecting, with very small nares located near its rim, separated from each other at a distance (INL/HW=0.09–0.16; Figs. 1 and 7A).

Description.—Carapace (Fig. 2) elongate, depressed, widest at marginals 7 or 8; three longitudinal rows of strong keels on carapace; medial row best developed; lateral row starting from near pleural 1 center in most adult animals (from contacting point of marginals 1 and 2 and

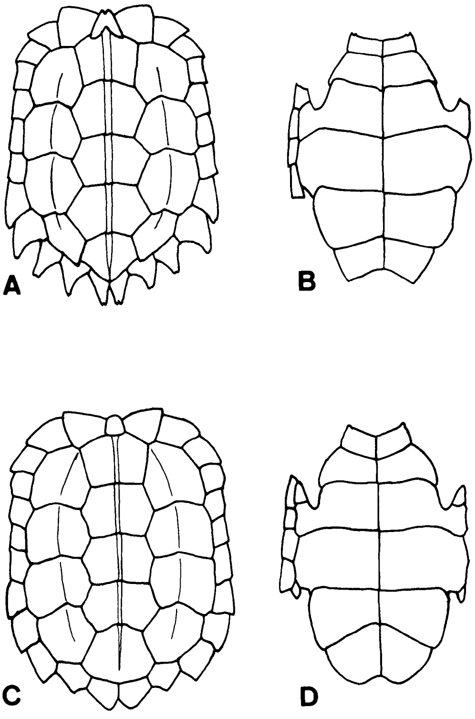

FIG. 2. Shells of *Geoemyda spengleri* (A, B) and *G. japonica* (C, D) in dorsal view of carapace (A, C) and ventral view of plastron (B, D)

pleural 1 in younger animals), slightly curving outward on pleural 1, terminating on pleural 3 (37/49), or extending to, but weak on, pleural 4 with no trace on bony plates underneath (12/49); posterior margin very strongly serrated, anterior margin also serrated but more weakly; such serration becoming weaker with age; cervical large, usually wedge-shaped, broader and notched posteriorly; each marginal with acute corner, marginals 1 and 2 anterolaterally and marginals 3–12 posterolaterally, mostly having single point (9–12 often strongly projecting backward), but corners of marginal 12 sometimes double pointed; vertebrals wider than long, third one widest; vertebral 1 widest anteriorly, the others widest medially; pleurals 1–3 as wide as adjacent vertebrals, pleural 4 smaller; marginals 11 and 12 often overlapped by posterior margin of pleural 4 and vertebral 5, respectively.

Surface of each carapacial scute rugose, with growth annuli; each vertebral and pleural with areola located near posterior margin along keel, growth annuli radiating forward from areola (Fig. 3); on cervical, areola located anteriorly; marginals 1–2 and 3–12 with areola located anterolaterally and posterolaterally, respectively; neurals 1 to 5 or 6 hexagonal, shortsided posteriorly; anterior part of pygal partly covered by marginal 12.

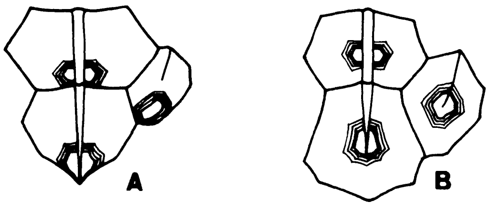

Fig. 3. Dorsal views of areolae and growth annuli in pleurals 4 and vertebrals 4 and 5 of *Geoemyda spengleri* (A), and *G. japonica* (B).

Plastron (Fig. 2) hingeless, large, elongated (PL2/CL2=0.78–0.93), laterally angulated, posterior margin with shallow but wide notch; anterior margin somewhat notched in adult, but very slight in juvenile; plastral formula: Ab> <P> <F>H> <An>G in most animals (42/46; Table 1); bridge short, dorsal border

Table 1. Plastral formulae of specimens of *Geoemyda spengleri* and *G. japonica* examined. Data for males, females and the specimens of unknown sexes are combined in total.

Plastral formula	*G. spengleri*			*G. japonica*		
	Male	Female	Total	Male	Female	Total
Ab>P>F>H>An>G	8	1	9			
P>Ab>F>H>An>G	4	2	6			
Ab>F>P>H>An>G	5	1	6			
P>Ab>F>An>H>G		5	5		1	1
P>F>Ab>H>An>G	3	2	5			
Ab>P>F>An>H>G	1	4	5		1	1
P>F>Ab>An>H>G		3	3			
F>P>Ab>H>An>G		2	2			
P>H>Ab>F>An>G	1		1			
Ab>H>F>P>An>G	1		1			
F>Ab>P>H>An>G	1		1			
Ab>F>H>P>An>G		1	1			
Ab>P>H>F>An>G	1		1			
Ab>P>An>F>H>G				9	3	15
P>Ab>An>F>H>G				2	6	10
P>Ab>An>F>G>H				2	4	6
Ab>P>An>H>F>G				1	1	2
P>Ab>An>H>F>G				1	1	2
P>An>Ab>F>H>G				1	1	2
P>An>Ab>H>F>G					1	1
P>An>H>An>F>G					1	1
An>P>An>G>H>F					1	1
Ab>P>F>An>H>G				1		1
P>An>Ab>G>F>H				1		1
P>Ab>An=F>G>H				1		1
Ab>P>An>F=H>G				1		1

nearly as broad as ventral border; axillary buttress moderate; inguinal buttress weak, barely reaching lateral margin of costals; entplastron posterior to gular-humeral seam, intersected by humero-pectoral seam; one specimen with a pair of very small axillaries, another with a pair of large and strange inguinals located more distally.

Head moderate in size, dorsal surface smooth, lacking subdivision into small scales; upper jaw unnotched, with medial hook; triturating surfaces of upper and lower jaws very narrow, without ridge and cusp; internal choanae marked by lateral ridges, lacking flaps and papillae (type C of Parsons, 1960, 1968); tongue broad, relatively thick, heart-shaped, covered with many small projections.

Anterior surfaces of forelimbs covered with enlarged, semispinose, imbricate scales; tips of the scales pointed, oriented distally; similar but slightly smaller scales covering heels of all limbs; small conical scales sparsely present on thighs and base of tail; toes less than one-third webbed, proportion of webbing variable; distal part of tail (posterior to vent) flat, with 5–14 pairs of square subcaudal scales, number of the pairs apparently decreasing with age probably because of neighboring fusion of scales and wear of tail tip.

Skull (Figs. 4 and 5) relatively flattened, elongate; orbit large, almost round but slightly longer than high; external naris wider above, upper and lower margins slightly projecting inward medially; fissura ethmoidalis narrow, keyhole-shaped; lower part (vomer sulcus) bordered by vomer, dorsal processes forked at each side, contacting prefrontal; right and left maxillae contacting each other anteriorly, forming a hooked beak; premaxilla bordering external naris anterodorsally; ventrolateral edge of maxilla slightly curving upward posteriorly, continuing to that of jugal without forming an angle; orbitonasal foramen small but penetrating ventrally; cranial cavity much narrowed anteroventrally, processus inferiores parietales closely approximated ventromedially, anterior end separated from palatine by pterygoid; foramen nervi vidiani on pterygoid, located posterolateral (2/4) or lateral to anterior end of processus inferior

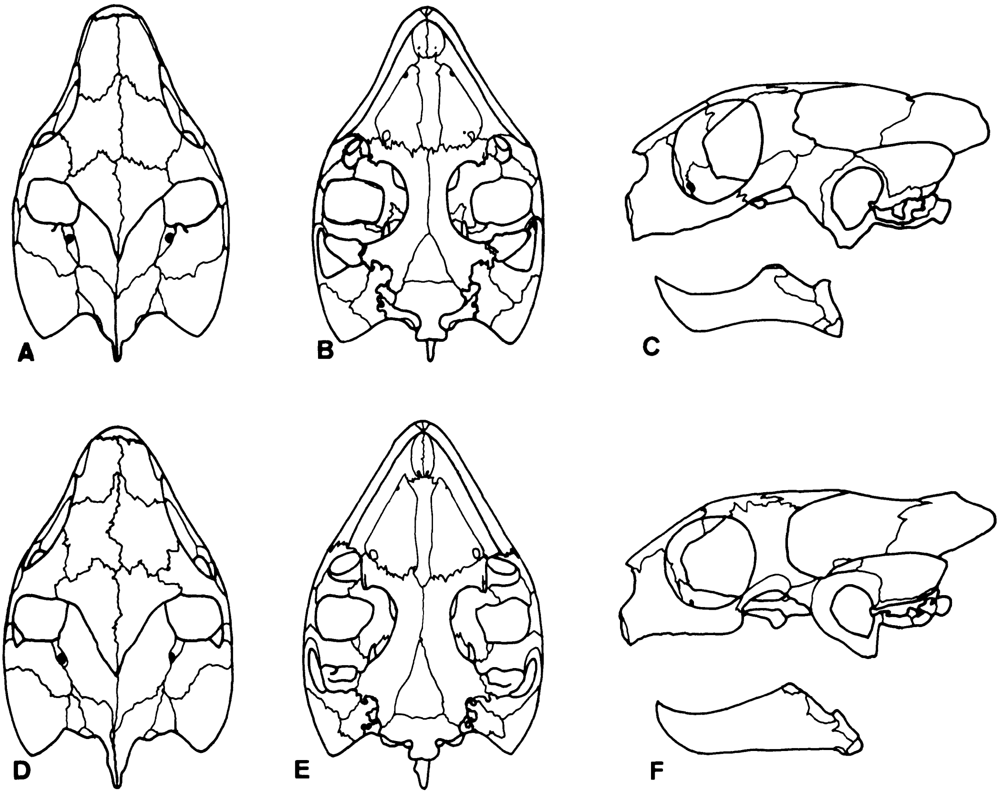

FIG. 4. Skulls of *Geoemyda spengleri* (A–C) and *G. japonica* (D–F) in dorsal (A, D), ventral (B, E) and lateral (C, F) view.

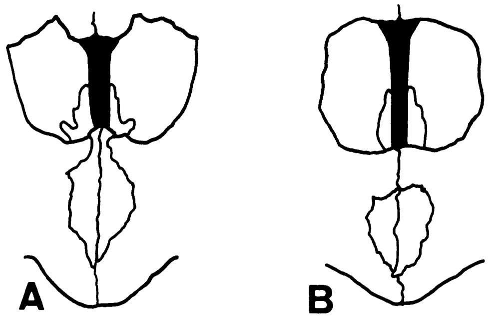

Fig. 5. Frontal view of bony beak and snout region of *Geoemyda spengleri* (A), and *G. japonica* (B). Solid black areas indicate the fissurae ethmoidalis.

parietalis (2/4); in former case the foramen near anterior end of epipterygoid; postorbital, jugal and quadratojugal contacting each other, forming weak temporal arch; quadratojugal much enlarged vertically, strongly compressed laterally, in contact with anterolateral part of squamosal; anterodorsal portion of quadrate forming major portion of weakly developed processus trochlearis oticum; prootic dorsal exposure reduced, with a little participation in the processus; anteroventral portion of quadrate slightly convex, visible dorsally; supraoccipital slightly projecting posteriorly; foramen palatinum posterius small, complete with maxillo-pterygoid contact (3/4), or incomplete without the contact (1/4); pterygoid weakly (2/4) or not contacting with jugal (2/4); processus pterygoideus externus indistinct; secondary plate not much developed; in upper and lower jaws, bony triturating surfaces narrow, ridgeless, without serration; ventral part of premaxilla relatively expanding, deeply concave; mandible thin, strongly curving upward into acute anterior tip; triturating surface of mandi-

Table 2. Allometric comparisons between sexes of *Geoemyda spengleri* and *G. japonica*. "–": $p>0.05$; "+": $p<0.05$; "⧺": $p<0.01$; and "⧻": $p<0.001$.

Character	*G. spengleri*		*G. japonica*	
	Sexual difference	Significance level	Sexual difference	Significance level
CL1	F>M	⧻	F=M	–
PL1	F>M	⧻	F>M	⧺
PL2	F>M	⧻	F>M	⧻
CW	F>M	⧻	F=M	–
SD1–2	F>M	⧻	F>M	⧻
SD2–3	F>M	+	F>M	⧻
SD4–5	F=M	–	F=M	–
DBL	F>M	⧻	F>M	⧻
VBL	F>M	⧻	F>M	⧻
APW	F>M	⧻	F>M	⧺
PPW	F>M	⧻	F>M	⧻
HW	F>M	+	F=M	–
CEL	F=M	–	F=M	–
CEW	F=M	–	F>M	+
V3W	F=M	–	F=M	–
V4W	F>M	+	F=M	–
V5W	F=M	–	F=M	–
V5L	F<M	⧻	F<M	⧻
V5Lm	F<M	⧺	F=M	–
P2L	F>M	⧻	F=M	–
P3L	F>M	⧻	F=M	–
GL	F=M	–	F=M	–
AnL	F>M	+	F=M	–
M12L	F<M	+	F=M	–
P4W	F=M	–	F=M	–
G	F=M	–	F=M	–
H	F<M	+	F>M	+
P	F>M	+	F>M	⧻
Ab	F=M	–	F=M	–
F	F=M	–	F=M	–
An	F>M	⧻	F=M	–

ble without horizontal part; coronoid poorly developed, only slightly visible laterally.

Coloration.—Carapace ground color variable, dark reddish orange, orange yellow, or moderate olive; connective tissue under scutes gray or reddish gray, forming very small, complicated fleck pattern; on carapace scutes, dark radiations occasionally partially present, dark lines or wedges extending along three longitudinal keels; bridge and plastron black or dark brown, the latter with narrow yellow or grayish yellow rim laterally; ground color of head and neck varying from olive brown or purplish gray to dark gray, with dark shadowy irregular patterns anterodorsally, more whitish on throat; limbs and tail similar to head in color, but with numerous whitish or reddish spots.

Sexual differences.—Midline carapace length (CL2) not significantly different between males and females; values of following measurements in relation to CL2 significantly greater in females than in males—CL1, CW, PL1, PL2, SD1-2: Fig. 7C, SD2-3, DBL, VBL, APW, PPW, P2L, P3L, AnL, AN, HW, P, and V4W; V5L, V5Lm, M12L, H in relation to CL2 significantly greater in males than in females (Table 2); plastron flat in females, slightly concave medially in males; males with very long (TL/CL2 = 0.44–0.59) and thick tail with vent far beyond carapacial rim; tail of females shorter (TL/CL2 = 0.27–0.42) and thinner, vent located close to or slightly beyond the rim; sexually dimorphic plastral kinesis (Moll, 1985) confirmed: two males and females osteologically examined having bony and ligamentous connection, respectively, between hypoplastron and carapace.

Juveniles (Rudloff, 1986) and females having white to yellowish or reddish narrow stripes and spots on posterior and lateral surfaces of head and neck; adult males having a patternless head, neck with or without indistinct patterns (Fig. 6); females and males showing yellowish or reddish and white or light gray iris, respectively; Smallest (CL2 = 72.5 mm) and second smallest males (CL2 = 77.7 mm) having a juvenile-like head patterns. The latter had a faintly reddish iris at first, but the reddish coloration disappeared, making the iris whitish, after a few weeks in captivity.

Variation.—See comparisons below.

Karyotypes.—2 n = 52 (Kamezaki and Ota, unpublished data).

Distribution.—Southeastern China (Kwangtung, Kwangsi and Hainan Is.) and eastern Indochina (Vietnam, ?Laos and ?Cambodia).

Ecological notes.—*Geoemyda spengleri* seems to be primarily terrestrial but occasionally enters streams (Fang, 1930). Pope (1935) considered its abundance in Yaoshan, reported by Fan (1931), as evidence that the turtle likes wild, wooded, montane environments. In captivity, it often enters shallow water but spends much more time on the ground (Petzold, 1963; Yasukawa's private observations).

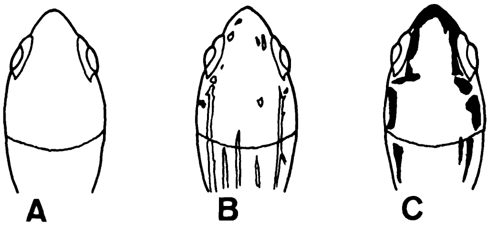

FIG. 6. Dorsal head patterns. A: male *Geoemyda spengleri*. B: juvenile and female *G. spengleri*. C: male and female *G. japonica*.

There have been no field observations on feeding habits of *G. spengleri*. In captivity, it feeds on various small invertebrates and vertebrates such as insects, earthworms, pink mice and meat. Some animals also feed on plant matter such as bananas and tomatos (Petzold, 1963; Rudloff, 1986; Yasukawa's private observations).

Rudloff (1986) reported that a captive female laid three single-egg clutches every thirty-eight days. The eggs were white, brittle-shelled, and much elongated, measuring 42–45 × 18 mm. One of them weighed 8.2 g. Incubation periods were 66 and 73 days in 28 C and 25 C, respectively. The shell of one hatchling measured 30 × 24 × 14 mm in length × width × height. In another captive case, a clutch of two eggs was laid, and they hatched after a 67-day incubation period at 30 C (Buskirk, private communication).

Geoemyda japonica Fan

Emys spengleri Okada, 1891 : 72.

Nicoria spengleri Anonymous, 1893 : 237; Fritze, 1894 : 859.

Geoemyda spengleri Stejneger, 1907 : 501; Fang, 1930 : 118 (part); Takashima, 1932 : 155; Fang, 1934 : 175 (part); Koba, 1957 : 196.

Geoemyda spengleri japonica Fan 1931 : 148; Pope, 1935 : 35; Nakamura and Uéno, 1963; Wermuth and Mertens, 1977 : 33; Ernst and Barbour, 1989 : 155; Iverson, 1992 : 123.

Holotype.—USNM No. 34053, an adult female collected at Nawa (?Naha), Okinawajima Is., Japan, by A. Owston.

Diagnosis.—Moderate-sized species of the Batagurinae $67.7 \leqq \mathrm{CL1} \leqq 163.5$ mm, $65.0 \leqq \mathrm{CL2} \leqq 155.7$ mm); with distinct pair of axillary scutes (50/50); mostly with a pair of small sometimes vestigial and scale-like inguinal scutes (30/33); but such rarely present only in one side (2/33); anterior and posterior margins of carapace serrated; plastron hingeless, notched anteriorly and posteriorly; midseam between femorals usually shorter than that between anals; plastron blackish, with light colored margin; snout not projecting, with nares located close to each other medially (INL/HW=0.04–0.09; Figs. 1 and 7A).

Description.—Carapace (Fig. 2) elongate, slightly doomed, rather flat-topped, widest at marginals 7 or 8; three longitudinal rows of strong keels on carapace, medial row best developed; lateral row starting from contacting point of marginal 1, vertebral 1 and pleural 1, greatly curving outward on pleural 1, reaching pleural 4, with trace on bony plates underneath; posterior margin strongly serrated, anterior margin also serrated but more weakly; such serration becoming weaker with age; cervical rather small to moderate in size, wedge-shaped or trapezoid, slightly broader with or without shallow notch posteriorly; each marginal with acute corners, marginals 1 and 2 anterolaterally and marginals 3–12 posterolaterally with single point; vertebrals mostly wider than long (vertebral 1 or 4 sometimes longer), widest ones usually vertebral 3 (27/42), 4 (10/42) or 5 (8/42); vertebral 1 widest anteriorly, vertebrals 2–4 medially, vertebral 5 posteriorly; pleurals large, as wide as adjacent vertebrals.

Surface of each carapacial scute rugose, with growth annuli; vertebrals 1–3 and pleurals 1–3 with areola located near posterior margin along keels, growth annuli radiating forward from areola; on vertebrals 4 (areola sometimes like vertebrals 1–3) and 5 and pleural 4 areola located slightly posterior to center along keels, growth annuli radiating out as concentric circles (Fig. 3); on cervical, areola located anteriorly; marginals 1 and 2 and 3–12 with areola located anterolaterally and posterolaterally, respectively; neurals 1 to 4, 5, or 6 hexagonal, shortsided posteriorly; pygal overlaid by marginals 12.

Plastron (Fig. 2) hingeless, large, elongate (PL2/CL2=0.78–1.00), laterally angulated, posterior margin with shallow, wide notch; anterior margin somewhat notched, not or only slightly notched in juvenile; plastral formula: P><Ab><An>F><H><G in most animals (41/46; Table 1); bridge short, dorsal

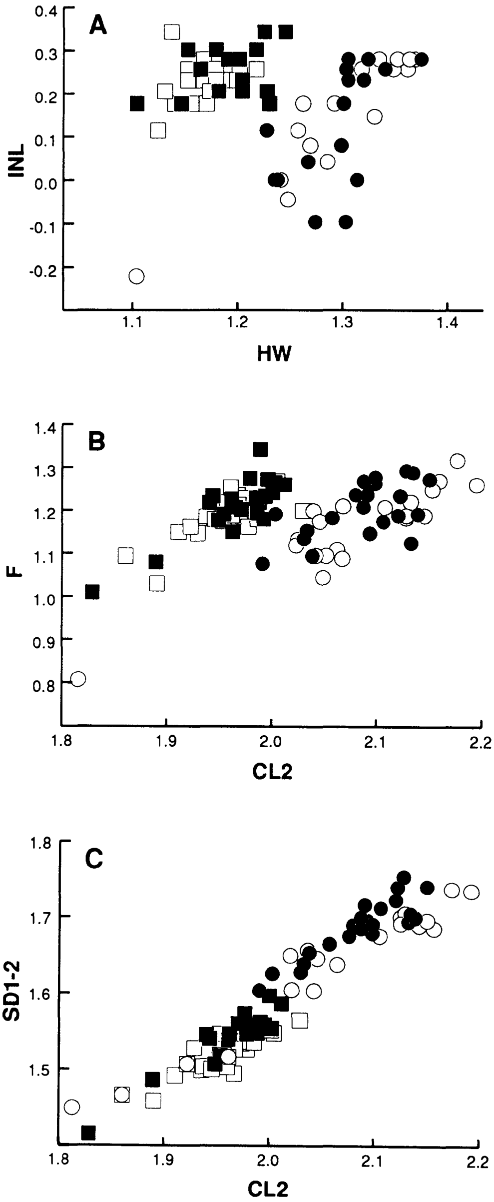

FIG. 7. Two dimensional plots of log-transformed scores of quantitative characters of *Geoemyda spengleri* and *G. japonica*. Each axis value is base 10 of logarithm. A: Internarial length (INL) against greatest head width (HW); B: midseam length of femorals (F) against midline length of carapace (CL2); C: shell depth between vertebrals 1–2 (SD1–2) against midline length of carapace (CL2). Open circle: male *G. spengleri*, closed circle: femele *G. spengleri*, open rectangle: male *G. japonica*, closed rectangle: female *G. japonica*.

border broader than ventral border; axillary buttress moderate; inguinal buttress weak, barely reaching lateral margin of costals; entoplastron posterior to gular-humeral seam, intersected by humeral-pectoral seam.

Head moderate in size, dorsal surface smooth, lacking subdivision into small scales; upper jaw unnotched, with a medial hook; triturating surfaces of upper and lower jaws very narrow, without ridge and cusp; internal choanae marked by lateral ridges, lacking flaps and papillae (type C of Parsons, 1960, 1968); tongue broad, relatively thick, heart-shaped, covered with many small projections.

Anterior surfaces of forelimbs covered with enlarged, semispinose, imbricate scales; tips of the scales roundish or slightly pointed, oriented distally; similar but slightly smaller scales covering also heels of hindlimbs; long, flexible, spiny scales present on thighs and base of tail in moderate to high densities; toes less than one-third webbed, proportion of webbing variable; distal part of tail (posterior to vent) flat, with 4–20 pairs of square subcaudal scales, number of the pairs apparently decreasing with age probably because of fusion of neighboring scales and wear of tail tip.

Skull (Figs. 4 and 5) relatively flattened, elongate; orbit large, almost round but slightly longer than high; upper margin of external naris as wide as its lower margin; fissura ethmoidalis narrow, keyhole-shaped; lower part (vomer sulcus) bordered by vomer, dorsal processes unforked at each side, contacting prefrontal; right and left maxillae contacting each other anteriorly,forming a hooked beak; premaxilla partly bordering external naris anterodorsally (1/3), or separated from the latter by intervention of upper part of maxilla (2/3); ventrolateral edge of maxilla forming an angle posteriorly under jugal; orbitonasal foramen very small, only slightly penetrating ventrally; cranial cavity much narrowed anteroventrally, processus inferiores parietales closely approximated ventromedially, anterior end separated from palatine and jugal by pterygoid; foramen nervi vidiani on pterygoid (2/3) or between pterygoid and parietals (1/3), located posterolateral (1/3) or lateral to anterior end of processus inferior parietalis (2/3); in former case the foramen near anterior end of epipterygoid; jugal and quadratojugal contacting each other, forming weak temporal arch; quadratojugal small, strongly compressed laterally, not contacting anterolateral part of squamosal; anterodorsal portion of quadrate forming major portion of well developed processus trochlearis oticum; prootic dorsal exposure reduced, with a little participation in the processus; anteroventral portion of quadrate slightly concave, invisible dorsally; supraoccipital slightly projecting posteriorly; foramen palatinum posterius small, complete with maxillo-pterygoid contact (1/3), or incomplete without the contact (2/3); pterygoid not contacting with jugal (2/3), or weakly contacting but only on left (1/3); processus pterygoideus externus prominent; secondary plate not much developed; in upper and lower jaws, bony triturating surfaces narrow, ridgeless, without serration; ventral part of premaxilla relatively expanding, with shallow concave; mandible thin, weakly curving upward into slightly acute anterior tip; triturating surface of mandible with narrow horizontal part; coronoid well developed, slightly projecting dorsally.

Coloration.—Carapacial ground color variable, deep orange, deep yellow, strong brown or reddish orange; connective tissue under scutes whitish without pattern; on carapace scutes, dark radiate or irregular spots mostly partially present, dark lines or wedges extending along longitudinal keels; bridge and plastron black or dark brown, the latter with light lateral rim, yellow or grayish yellow in others, light reddish orange in hatchlings; ground color of head and neck varying from orange yellow to yellowish or reddish brown, with irregular but subsymmetrical reddish or yellowish lines or spots on snout, and lateral surface of head and neck (Fig. 6); anterodorsal surface of head excepting snout with dark irregular pattern; throat darker in ground color, with small reddish or whitish spots; iris yellowish or reddish brown, or reddish gold; limbs and tail dark reddish brown, purplish black, or black, partly with reddish or yellowish lines or spots.

Sexual differences.—Midline carapace length (CL2) not significantly different between males and females; values of following measurements in relation to CL2 significantly greater in females than in males—PL1, PL2, SD1–2: Fig. 7C, SD2–3, DBL, VBL, APW, P, PPW, and H; plastron flat in females, slightly concave medially in males; males with very long ($TL/CL2=0.32$–0.58) and thick tail with the vent far beyond carapacial rim; tail of females shorter ($TL/CL2=0.23$–0.41) and thinner, vent located close to or slightly beyond the rim; sexually dimorphic plastral kinesis (Moll, 1985) confirmed: two females osteologically examined had a ligamentous connection between hypoplastron and carapace, whereas a shell had a concave plastron (male feature) had a bony connection there.

Sexual dimorphism not evident in coloration, but in some males, carapace and head more reddish than in females or other males.

Variation.—See comparisons below .

Karyotypes.—2n = 52 (Nakamura, 1949).

Distribution.—Okinawajima, Kumejima, and Tokashikijima Is., of the Okinawa Group central RyuKyus, Japan.

Ecological notes.—Geoemyda japonica is found chiefly on the forest floor (Nakamura and Uéno, 1963; Takara, 1969). Nakamura and Uéno (1963) stated that the species is herbivorous. But this turtle is known to prey also on small invertebrates such as insects, earthworms and snails as well (Takara, 1969; Ota unpublished data).

Very little information is available regarding the reproductive habits of *G. japonica*. Takara (1969) stated that this turtle lays 4–6 eggs, approximately 45 mm in length, from June to August, but without providing any concrete data. Otani (1989) briefly reported two cases of captive breeding of *G. japonica*. In one case, a single egg (46.1 × 29.2 mm and 15.8 g in major × minor diameters and weight, respectively) was laid on 7 April, and hatched on 31 July of the same year, the hatchling measured 35.5 × 33.2 × 17.2 mm in length × width × height, and weighed 8.8 g. Another egg (46.3 × 23.2 mm, 16.1 g) was laid on 1 May, and hatched on 14 July. The hatchling of the latter measured 35.6 × 28.1 × 17.0 mm in shell length × width × height, and weighed 8.9 g.

Comparisons

Quantitative Characters

Midline carapace length (*CL2*).—No sexual differences are evident in adult CL2 within *G. spengleri* or *G. japonica* ($p > 0.05$). The CL2 in adult *G. japonica* is significantly greater than in adult *G. spengleri* ($p < 0.0001$).

Internarial length (*INL*).—There are no significant differences in the adult INL in relation to HW between the sexes within each species. Significant interpecific difference exists in slope ($p < 0.05$; Fig. 7A). INL/HW varies 0.09–0.16 in *G. spengleri*, whereas 0.04–0.09 in *G. japonica*.

Tail length (*TL*), *postcloacal tail length* (*VTL*).—In both species, adult TL and VTL in relation to CL2 are highly variable within each sex, probably resulting from various degrees of tail tip wear among individuals within each species. There are no distinct interspecific differences in these characters. In the both species, the intersexual differences of adult TL is distinct , and males have a much longer tail than females: TL/CL2 = 0.44–0.59 in male G. spengleri, 0.27–0.42 = in female *G. spengleri*, 0.32–0.58 in male *G. japonica*, and 0.23–0.41 in female *G. japonica*.

Adult morphometric characters without sexual difference in each species.—These characters were compared for all adult specimens between *G. spengleri* and those of *G. japonica* (Table 3). CEL, CEW and F (Fig. 7B) in relation to CL2 are significantly greater in *G. spengleri* than in *G. japonica*, whereas SD4–5, GL, G and P4W in relation to CL2 are significantly greater in the latter than in the former. *G. spengleri* shows greater relative CEL, CEW and F, and smaller relative SD4–5, GL, G and P4W than *G. japonica*. There are no significant differences in V3W, V5W and AB between *G. spengleri* and *G. japonica*.

Adult morphometric characters with sexual differences in one or both of the two species.—These characters were compared between *G. spengleri* and *G. japonica* separately in males and females (Table 4). In both sexes, P3L and V4W in relation to CL2 are significantly greater in *G. spengleri* than in *G. japonica*, whereas SD1–2 (Fig. 7C), SD2–3, M12L and An in relation to CL2 are significantly greater in the former than in he former. *G. spengleri* shows greater relative P3L and V4W, and smaller relative SD1–2, SD2–3, M12L and An than *G. japonica*. Though relative V5L is not significantly different between species, *G. japonica* has significantly

Table 3. Allometric comparisons between *Geoemyda spengleri* (S) and *G. japonica* (J) for characters showing no sexual differences within each species. "–": $p > 0.05$; "+": $p < 0.05$; "⧺": $p < 0.01$; and "⧻": $p < 0.001$. See text for methods of analyses.

Character	Interspecific difference	Signiffcant level
CL2	S<J	⧻
SD4–5	S<J	⧻
CEL	S>J	⧻
CEW	S>J	⧻
GL	S<J	⧻
V3W	S=J	–
V5W	S=J	–
P4W	S<J	⧻
G	S<J	⧻
AB	S=J	–
F	S>J	⧻

TABLE 4. Allometric comparisons between *Geoemyda spengleri* (S) and *G. japonica* (J) for characters showing sexual differences in one or both of the species. "−": $p>0.05$; "+": $p<0.05$; "⧺": $p<0.01$; and "⧻": $p<0.001$. See text for methods of analyses.

Character	Female		Male	
	Interspecific difference	Significance level	Interspeciffc difference	Significance level
CL1	S=J	−	S>J	⧺
PL1	S>J	⧺	S=J	−
PL2	S=J	−	S=J	−
CW	S=J	−	S=J	−
SD1–2	S<J	⧻	S<J	⧻
SD2–3	S<J	⧻	S<J	⧻
DBL	S=J	−	S<J	⧻
VBL	S>J	⧻	S=J	−
APW	S=J	−	S=J	−
PPW	S=J	−	S=J	−
HW	S=J	−	S<J	⧻
V4W	S>J	⧻	S>J	+
V5L	S=J	−	S=J	−
V5Lm	S<J	⧻	S<J	⧻
P2L	S=J	−	S<J	+
P3L	S>J	⧻	S=J	−
AnL	S=J	−	S<J	+
M12L	S<J	⧻	S<J	⧻
H	S=J	−	S>J	⧻
P	S=J	−	S<J	+
An	S<J	⧻	S<J	⧻

greater V5Lm in relation to both CL2 and V5Lm ($p<0.001$ in y-intercept; $p>0.05$ in slope) than *G. spengleri* in both sexes. In *G. japonica*, widest portion of vertebral 5 is more posteriorly located when compared with that in *G. spengleri*.

No significant interspecific differences are recognizable in PL2, CW, VT, APW, and PPW.

In males, CL1 and H in relation to CL2 are significantly greater in *G. spengleri* than in *G. japonica*, whereas DBL, HW, K2 and P in relation to CL2 are significantly greater in the latter than in the former. *G. spengleri* shows greater relative CL1 and H, and smaller relative DBL, HW, K2 and P than *G. japonica*. These characters show no significant interspecific differences in females.

In females, PL1 and VBL in relation to CL2 are significantly greater in *G. spengleri* than in *G. japonica*. *Geoemyda spengleri* shows greater relative PL1 and VBL than *G. japonica*. These characters show no significant interspecific differences in males.

Qualitative characters

Differences in qualitative characters between the two species are summarized in Table 5. Since the evaluation by Pope (1935), the presence or absence of the axillary has been considered as a valid character to separate the two forms of *Geoemyda*, and the present results also support this account: almost all *G. spengleri* (47/49) had no axillary and inguinal, whereas all *G. japonica* had a prominent pair of axillaries (Fig. 2). Most of the specimens of *G. japonica* (30/33) also had a pair of small (sometimes soft and vestigial) inguinals. One specimen of *G. spengleri* showed a pair of very small scutes in the position of axillaries, but their sizes suggest that they were produced by aberrant development. Thus, the absence or presence of the axillary can be an especially good discriminant character for *G. spengleri* and *G. japonica*.

The shell and scute morphology also distinctly differs between *G. spengleri* and *G. japonica*. A large number of differences are recogninizable especially in posterior scutes (Figs. 2 and 3). The shape and size of vertebrals 4 and 5 and pleurals 3 and 4 show considerable differences between the species. *G. spengleri* has very small pleural 4 with no or very weak keel, and even in the latter case, there is no trace of keel on the bony plates underneath. In *G. japonica*, pleural 4 is large with prominent keel involving traces on bony plates. The pygal reaches vertebral 5 in *G. spengleri*, whereas not in *G. japonica*. *Geoemyda spengleri* has areolae (embryonic

TABLE 5. Comparisons of qualitative characters between *Geoemyda spengleri* and *G. japonica*

Character	*Geoemyda spengleri*	*Geoemyda japonica*
Cervical scute	large	rather small or moderate
Vertebral 5 (V5)	widest medially	widest posteriorly
areola on V5	located posteriorly	located medially
Widest vertebral	V4	V3, V4, or V5
Pleural 4 (P4)	smaller than other pleurals	as wide as adjacent vertebrals
areola on P4	located posteriorly	located medially
Keels on P4	weak or absent	prominent
Keels on costals under P4	without trace on bony plates	with trace on bony plates
Pygal	covered by vertebral 5	not covered by vertebral 5
Paired axillary scutes	absent	present
Paired inguinal scutes	absent	present
Plastral midseam	femoral>anal	anal>femoral
Size of external naris (EN)	very small	moderate
Relative location of ENs	separated for a distance	closely located
Large scales on forelimbs	with acute tip	with roundish tip
Semispinose scales on thighs and base of tail	short, conical, and sparsely present	long, spiny, and often densely present
Processus coronoideus	indistinct	prominent
P. pterygoideus externus	indistinct	prominent
P. trochlearis oticum	poorly developed	well developed
Vomer under vomer sulcus	forked at either side	not forked at either side
Ventrolateral part of maxilla	not projecting posteriorly	projecting posteriorly
Triturating surface of mandible	without horizontal surface	with horizontal surface
Sexual color differences	present	absent
Connective tissue under carapace scutes	grayish or reddish and with complicated fleck pattern	whitish and patternless

scute areas: Obst, 1986) near posterior margins of vertebrals and pleurals. On the other hands, areolae are located only slightly posterior to the center in vertebrals 4 and 5 and pleural 4 in *G. japonica* (Fig. 3). The location of the areola and the shape of radiation of growth annuli around it reflects the growth direction and rate of the scute (Zangerl, 1969; Moll and Legler, 1971).

Considerable interspecific differences are present also in the plastral formula. Both *G. spengleri* and *G. japonica* exhibit varieties of formulae, of which, however, only two are common to them (Table 1). *G. spengleri* has the midseam between femorals longer than that between anals (46/46). By contrast, anal midseam is usually longer than femoral midseam in most *G. japonica* (41/46).

The size and location of external nares are strikingly different between *G. spengleri* and *G. japonica* (Figs. 1 and 7A). In *G. spengleri*, nares are very small, and are located near lateral rims of anterior surface of the snout and separated from each other at a distance. *Geoemyda japonica*, on the other hand, has moderate sized nares, closely located to each other near the center of the snout. But both of these species have internal choanae which are laterally marked by ridges and lack papillae and flaps (ie., type C of Parsons, 1960, 1968).

This study also revealed differences in several skeletal characters between *G. spengleri* and *G. japonica* (Fig. 4). In the latter species, the processus coronoideus, p. trochlearis oticum, and p. pterygoideus externus are better developed, whereas elements composing the temporal arch, especially the quadratojugal, are less developed when compared with those in the former. The anteroventral portion of the quadrate is slightly concave under the p. trochlearis oticum in *G. japonica*, whereas that of *G. spengleri* is slightly convex there. The musculus adductor mandibularis externus attaches to the p. coronoideus and turns around on the p. trochlearis oticum, and m. pterygoideus pars dorsalis attaches to the pterygoid along the p. pterygoideus externus. Therefore, the greater development of these three processes in *G. japonica* is probably associated with the higher development of masticatory muscles in this species. The reduction of the temporal arch and the anteroventral concave of the quadrate also enable masticatory muscles to develop better. In *G. japonica*, the ventrolateral part of the maxilla projects slightly posteriorly; it thus, due to the narrow horizontal triturating surface on the mandible, increases the upper and lower triturating surfaces. On the other hand, *G. spengleri* has neither of these structures on the maxilla and the mandible. The anterior end of the mandible is much more curved dorsally, and the premaxilla, meeting the tip of the mandible, is dorsally more concave in *G. spengleri*. The vomer is not forked at all in *G. japonica*, whereas it is forked under the vomer sulcus in *G. spengleri* (Fig. 5).

Sexually associated color variation is known only in a few batagurine turtles (Pritchard, 1979; Ernst and Barbour, 1989). Juveniles of *G. spengleri* have light color stripes and spots on the head and neck (Rudloff, 1986), and only males lose such markings with growth (Fig. 6). Obst (1986) reported that the iris is yellow-orange in males and whitish in females. However, this description is misleading, because all living male (N=23) and female (N=12) specimens examined except one small male conversely had a white or light gray and a yellowish or reddish iris, respectively. Probably juveniles of *G. spengleri* have a female-like iris, but it turns white or gray only in adult males. The loss of light markings accompanying melanism is known in old males of some turtles, such as *Chinemys reevesii* (Gray) (Ernst and Barbour, 1989). But older males of *G. spengleri* without markings are not melanized. Such ontogenetic color variations are absent in *G. japonica*.

In *G. spengleri*, the connective tissue lining the carapacial scutes forms a pattern of very small and complicated grayish or reddish flecks. The color and shade of those patterns make carapacial coloration of this turtle variable. The connective tissue of corresponding portions are whitish without pattern in *G. japonica*.

DISCUSSION

There are numerous arguments regarding the criteria for application of the species category in herpetology, and very little consensus seems to have yet been attained among researchers, especially on the taxonomic treatment of allopatric populations [see Frost and Hills (1990) for review]. However, considering the small number of diagnostic characters and the slight degree of their differences among some recognized testudine species [e.g., those between *Cuora flavomarginata* and *C. evelynae* provided by Ernst and Lovich (1990); see Ernst and Barbour (1989) for numerous other examples], we believe that, although their monophyly is likely (see below), the above-mentioned differences between *G. spengleri* and *G. japonica* are strongly in favor of treating them as distinct species, and that none support their retention any longer as conspecific subspecies. The geographic distance of their ranges, obviously reflecting their long-term isolation from each other, supports this view circumstantially.

The current systematics of the subfamily Batagurinae still poses numerous problems even at the alpha-level (Gaffney and Meylan, 1988). The status of the genus *Geoemyda* is unstable without an established consensus among taxonomists. McDowell (1964), mainly on the bases of cranial characters, divided the family Emydidae into Emydinae and Batagurinae. He further divided the latter into four groups, of which the *Geoemyda* complex, characterized by a narrow, ridgeless triturating surface, consists of *Geoemyda, Melanochelys, Heosemys, Rhinoclemmys, Cuora, Cyclemys* and *Notochelys*. McDowell (1964) assigned three species, *spengleri* (subspecific epithet lacking), *mouhotii* and *flavomarginata* to *Geoemyda*, chiefly on the basis of the ventrally narrowed cranial cavity. The three turtles, however, actually greatly differ from each other, as he stated in the same paper, and *mouhotii* and *flavomarginata* are usually placed in *Pyxidea* and *Cuora*, respectively (Ernst and Barbour, 1989). *Pyxidea mouhotii* differs from *G. spengleri* and *G. japonica* in having a hinged plastron, large scales on the posterior part of head, broad triangular ethmoid fissure, and the foramen palatinum posterius excluded from the pterygoid (Table 6), whereas *C. flavomarginata* has a well-developed plastral hinge and closing mechanism, and lacks the quadratojugal (Hirayama, 1984; Ernst and Barbour, 1989). Based on these characters, Hirayama (1984) assumed that *C. flavomarginata* is most closely related to *C. galbinifrons* (Bourret), a species having little narrowed cranial cavity and a well-developed plastral hinge.

Hirayama (1984), on the other hand, considered *Pyxidea mouhotii* as the sister group of *Geoemyda* without discriminating *G. spengleri* and *G. japonica*. He revealed five characters as the synapomorphy of *G. spengleri* and *P. mouhotii* against the other members of the *Geoemyda* complex sensu McDowell (1964): ventrally narrowed cranial cavity (processus inferiores parietales close to each other ventromedially), marginal serration of peripheral plates, separation of jugal from pterygoid, foramen nervi vidiani located posterolateral to anterior end of processus inferior parietalis and bordered by parietal, palatine and epipterygoid,

TABLE 6. Comparisons of *Geoemyda spengleri* and *G. japonica* with *Pyxidea mouhotii, Heosemys silvatica, H. spinosa*, and *H. grandis*. "+" indicates the character is present. "−" absent and "±" variable. States of all characters of *G. spengleri* and *G. japonica* were directly observed in the present study. Data for all characters of *H. silvatica*, cloacal bursae condition and penial morphology of *H. spinosa*, and cloacal bursae condition in *H. grandis* were taken from Moll et al. (1986). Sexual dimorphic plastral kinesis in *H. spinosa* was based on Moll (1985). States of the other characters are based on Yasukawa's unpublished data.

Character	*Geoemyda spengleri*	*G. japonica*	*Pyxidea mouhotii*	*Heosemys silvatica*	*H. spinosa*	*H. grandis*
Axillary scute	−	+	±	±	+	+
Hooked beak without notch	+	+	+	+	−	−
Maxillae contacting anteriorly constituting a hooked beak	+	+	−	+	−	−
Pterygoid not contacting jugal	±	±	+	+	−	−
Small foramen posterius palatinum with pterygoid participation	+	+	−	−	−	−
Fissura ethmoidalis relatively narrow and keyhole-shaped	+	+	−	−	−	−
Choanae marked by ridges	+	+	+	+	−	−
Carapace with 3 prominent keels	+	+	+	+	−	−
Cloacal bursae	−	?	−	−	+	+
Adult animals with plastral hinge	−	−	+	−	−	−
Sexual dimorphic plastral kinesis	+	+	−	+	+	?
Quadratojugal (postorbital bar)	+	+	+	−	−	−
Ventrally narrowed cranial cavity	+	+	+	±	−	−
Posterior margin of carapace strongly serrated	+	+	+	−	+	+
Humero-pectoral seam transverses entoplastron	+	+	+	−	+	+
Protic exposure reduced dorsally	+	+	+	−	−	−
Posterior head skin not dividing to scales	+	+	−	−	−	−
Large bony shingle-like scutes on forelimbs	+	+	+	+	+	+
Enlarged scutes on the soles	+	+	+	+	+	+
Knob-like prominences on plica media lateralis of penis	+	+	+	+	+	+

and absence of cloacal bursae. In the present study, ventrally narrowed cranial cavity and marginal serration of peripheral plates have been confirmed in both *G. spengleri* and *G. japonica*. Separation of jugal from pterygoid is observed in some specimens but not in others (2/4 in *G. spengleri*, and 2/3 in *G. japonica*): jugal weakly contacting pterygoid on both sides in two specimens of *G. spengleri*, and on left side in one specimen of *G. japonica*. The position of foramen nervi vidiani is highly variable. In *G. spengleri*, the foramen is located posterolateral (2/4) or lateral to the anterior end of processus inferior parietalis (2/4), whereas it is posterolateral (1/3) or lateral (2/3) in *G. japonica*. The palatine is excluded from the parietal by the pterygoid in both *G. spengleri* and *G. japonica*. Thus, the foramen is located on the pterygoid (4/4 and 2/3 in *G. spengleri* and *G. japonica*, respectively) or between the pterygoid and parietals (1/3 in *G. japonica*). When the foramen is located posterolateral to the anterior end of the processus, its location is close to the anterior end of the epipterygoid. Absence of cloacal bursae was confirmed in *G. spengleri*, but was not examined for *G. japonica* (Table 6). Thus, Hirayama's (1984) assumption on the monophyly of *P. mouhotii* with *G. spengleri* and *G. japonica* requires further verification.

Moll et al. (1986) compared *Heosemys silvatica* (Henderson), a rare Indian species generally assigned to the genus presumably on the basis of the lack of quadratojugal (McDowell, 1964), with *H. spinosa* (Gray), *H. grandis* (Gray) and *G. spengleri* (without subspecific epithet or locality data), and reassigned the species to *Geoemyda*. They noted that *H. silvatica* is similar to *G. spengleri* in having a hooked beak consisting exclusively of the maxilla (unhooked beak with premaxilla participation in *H. spinosa* and *H. grandis*), three prominent carapacial keels (only a medial or no prominent keels in other *Heosemys*), and internal choanae marked by lateral ridges and lacking flaps and papillae (type C of Parsons, 1960, 1968). Internal choanae of *H. spinosa* and *H. grandis* have no special structure along the lateral border of the choanae (type D of Parsons, 1960, 1968). But besides the loss of the quadratojugal, *H. silvatica* differs from *G. spengleri* and *G. japonica* in having unserrated carapace, the entoplastron not transversed by the humero-pectoral seam, and the processus trochlearis oticum mainly consisting of the greatly exposed prootic (Moll et al., 1986). In *G. spengleri* and *G. japonica*, the prootic exposure is reduced and the processus is mainly composed of the quadrate (Table 6). Therefore the reassignment of *H. silvatica* to the genus *Geoemyda* seems to be premature, and we believe that it is currently appropriate to retain the species in *Heosemys*.

As is revealed in the present study, *G. spengleri* and *G. japonica* are distinct from each other in several characters. Even so, however, they still share many exclusive features. *P. mouhotii* and *H. silvatica* may possibly be closely related to the two species, but their phylogenetic allocation between *spengleri* and *japonica* seems unlikely (see above), suggesting monophyly of the latter two species. Moreover, problems regarding the monophyly of *spengleri* and *japonica* with at least one of the former two species remain unsolved. Thus, we at present define the genus *Geoemyda* as consisting only of *spengleri* and *japonica*. Detailed analyses using more characters of wider range of taxa are needed to infer phylogenetic relationships of *Geoemyda* and other batagurine genera appropriately.

ACKNOWLEDGMENTS.—We wish to express our gratitude to R. Aoki, Y. Chigira (OPM), R. Hirayama, N. Ichikawa (Himeji City Aquarium), A. Kamata, T. Otani (Zoo Okinawa), Y. Shibata (OMNH), M. Toyama, R. I. Crombie, W. R. Heyer, A. H. Wynn, and G. R. Zug (USNM) for allowing us to examine specimens in their care, and S. Ikehara for providing precious specimens. R. Aoki, J. Buskirk, R. Hirayama, I. Ineich, A. Mori, S. Sengoku, and Y. Shibata provided important literature and information. N. Kamezaki allowed use of unpublished data. M. Amano helped with computer analyses. We are also much indebted to J. Buskirk, H. Smith, and M. Tasumi for critically reading an early draft. This research was partially supported by U.S. National Geographic Society Fund (No. 4505–91 to M. Matsui), and a Grant-in-Aid from Japan Ministry of Education, Science, and Culture (A-63790257 to H. Ota).

LITERATURE CITED

ANONYMOUS. 1893. Untitled addendum. Proc. Zool. Soc. London 1893 : 237.

BORY DE ST. VINCENT, J. B. G. M. 1804. Voyage dans les quatre principales îles des mers d'Afrique, fait... (1801–1802)... sur la corvette "Le Naturaliste" dans l'expédition de découvertes commandée par le Capitaine Baudin. 3 v. Atlas. (not examined; from Bourret, 1941)

BOULENGER, G. A. 1889. Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History). Taylor and Francis, London. 311 p.

BOURRET, R. 1941. Les tortues de l'Indochine. Inst. Océanograph. l'Indochine., Nhatrang. 235 p.

ELERA, C. 1895. Catálogo systemático de toda la fauna de Filipinas, Vol. 1. Vertebrados, p. 399–454, Manila. (not examined; from Taylor, 1920)

ERNST, C. H. AND R. W. BARBOUR. 1989. Turtles of the World. Smithsonian Ins. Press, Washington, D. C. 313 p.

ERNST, C. H. AND J. E. LOVICH. 1990. A new species of *Cuora* (Reptilia: Testudines: Emydidae) from Ryukyu islands. Proc. Biol. Soc. Washington. 103(1) : 26–34.

FAN, T. H. 1931. Preliminary report of reptiles from Yaoshan, Kwangsi, China. Bull. Dept. Biol. Coll. Sci. Sun Yatsen Univ. (11) : 1–154.

FANG, P. W. 1930. Notes on chelonians of Kwangsi, China. Sinensia 1 : 95–135.

FANG, P. W. 1934. Notes on some chelonians of China. Sinensia 4 : 145–199.

FRITZE, A. 1894. Die Fauna der Liu-kiu-Insel Okinawa. Zool. Jahrb. Syst. 7 : 859.

FROST, D. R., AND D. M. HILLIS. 1990. Species in concept and practice: Herpetological applications. Herpetologica 46 (1) : 87–104.

FUKUDA, T. 1965. 500 Color Cards. Koshin Shobo, Tokyo. (In Japanese)

GAFFNEY, E. S. 1979. Comparative cranial morphology of Recent and fossil turtles. Bull. Am. Mus. Nat. Hist. 164 : 65–376.

GAFFNEY, E. S. AND P. MEYLAN. 1988. A phylogeny of turtles. *In*: M. J. Benton (ed.), The Phylogeny and Classification of the Tetrapods, Vol. 1. p.157–219. Oxford Univ. Press, New York.

GMELIN, J. F. 1789. Caroli a Linné, Systema naturae per regna tria natural, secondum classes, ordines, genera, species cum characteribus differentiis, synonymis, locis. 1(3) : 1038–1516.

GRAY, J. E. 1834. Characters of several new species of freshwater tortoises (*Emys*) from India and China. Proc. Zool. Soc. London. 1834 : 99–100.

GRAY, J. E. 1855. Catalogue of Shield Reptiles in the Collection of the British Museum. Part 1. Testudinata (tortoises). Taylor and Francis, London. 79 p.

Hirayama, R. 1984. Cladistic analysis of batagurine turtles (Batagurinae: Emydidae: Testudinoidea); a preliminary result. Stud. Geol. Salama. Spl. Vol. 1 : 141–157.

Iverson, J. B. 1986. A Checklist with Distribution Maps of the Turtles of the World. Privately printed, Richmond, Indiana. 283 p.

Iverson, J. B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Privately printed, Richmond, Indiana. 363 p.

Koba, K. 1957. Reptiles and Amphibia of Okinawa-jima of the Loo Choo Islands. Bull. Fac. Educ. Kumamoto Univ. 5 : 191–208. (in Japanese, with English summary)

Latreille, P. A. 1802. Untitled addendum. *In*: C. N. S. Sonnini de Manoncourt and. P. A. Latreille, Histoire Naturelle des Reptiles. Vol. 1, Paris. 280 p. (not examined; from Bourret, 1941)

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, and C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985(3) : 802–832.

Lovich, J. E. and C. H. Ernst. 1989. Variation in the plastral formulae of selected turtles with comments on taxonomic utility. Copeia 1989(2) : 304–318.

McDowell, S. B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proc. Zool. Soc. London 143 : 239–279.

Moll, E. O. 1985. Comment: sexually dimorphic plastral kinesis—the forgotten papers. Herpetol. Review 16(1) : 16.

Moll, E. O. and J. M. Legler. 1971. The life history of a neotropical Slider turtle, *Pseudemys scripta* (Schoepff), in Panama. Bull. Los Angeles Co. Mus. Nat. Hist. Sci. (11) : 1–102.

Moll, E. O., B. Groombridge and J. Vijaya. 1986. Redescription of the cane turtle with notes on its natural history and classification. J. Bombay Nat. Hist. Sc., Suppl. 83 : 112–126.

Nakamura, K. 1949. A study of chromosomes in some chelonians with notes on chromosomal formula in the Chelonia. Sensyokutai (La Kromosomo) 5/6 : 205–213. (in Japanese, with English résumé)

Nakamura, K. and S.-I. Uéno. 1963. Japanese Reptiles and Amphibians in Colour. Hoikusha, Osaka. 214 p. (in Japanese)

Obst, F. J. 1986. Turtles, Tortoises and Terrapins. St. Martin's Press, New York. 231 p.

Okada, S. 1891. A Catalogue of Vertebrated Animals of Japan. Kinkodo, Tokyo. 128 p. (not examined; from Takashima, 1932)

Otani, T. 1989. Growth of artificially hatched juveniles of *Geoemyda spengleri japonica* in captivity. Akamata (6) : 7–8. (in Japanese)

Parsons, T. S. 1960. The structure of the choanae of the Emydinae (Testudines, Testudinidae). Bull. Mus. Comp. Zool. 123(4) : 113–127.

Parsons, T. S. 1968. Variation in the choanal structure of recent turtles. Can. J. Zool. 46 : 1235–1263.

Petzold, H. G. 1963. Über einige Schildkröten aus Nord-Vietnam im Tierpark Berlin. Senckenb. Biol. 44 : 1–20.

Pope, C. H. 1934. List of Chinese turtles, crocodilians, and snakes, with keys. Am. Mus. Novit. (733) : 1–29.

Pope, C. H. 1935. Natural History of Central Asia. Vol. 10. The Reptiles of China. Am. Mus. Nat. Hist., New York. 604 p.

Pritchard, P. C. 1979. Encyclopedia of Turtles. T. F. H. Publ., Neptune, New Jersey. 895 p.

Rooij, N. 1915. The Reptiles of the Indo-Australian Archipelago. Vol. 1. Lacertilla, Chelonia, Emydosauria. E. J. Brill, Leiden. 384 p.

Rudlo, H. W. 1986. Beitrag zur Kenntnis der Zacken-Erdschildkröte *Geoemyda spengleri spengleri* (Gmelin, 1789). Herpetofauna 8(40) : 14–20.

SAS, 1985. User's Guide: Statistics, Version 5ed. SAS Institute Inc., Cary, North Carolina. 956 p.

Schweigger, A. F. 1814. Prodromi monographæ Cheloniorum sectio prima. Regiomontæ. (not examined; from Bourret, 1941)

Shaw, G. 1802. General Zoology (Reptiles, T. 3). London. (not examined; from Bourret, 1941)

Siebenrock, F. 1906. Zur Kenntnis der Schildkrötenfauna der Insel Hainan. Zool. Anz. 30 : 578–586.

Siebenrock, F. 1907. Über einige, zum Teil seltene Schildkröten aus Südchina. Sitz. Akad. Wiss. Wien. Math.-natur. Kl. Abt. 1. 116 : 1741–1776.

Siebenrock, F. 1909. Synopsis der rezenten Schildkröten mit Berücksichtigung der in historischer Zeit aus gestorbenen Arten. Zool. Jahrb. Suppl. 10 : 427–618.

Smith, M. A. 1931. The Fauna of British India, including Ceylon and Burma. Reptiles and Amphibia, vol. 1, Loricata and Testudines. Taylor and Francis, London. 185 p.

Stejneger, L. H. 1907. Herpetology of Japan and adjacent territory. Bull. U. S. Nat. Mus. 58 : 1–577.

Strauch, A. 1862. Chelonologische Studien, mit besonderer Beziehung auf die Schildkrötensammlung der Kaiserlichen Akademie der Wissenschaften zu St. Petersbourg. Mém. Acad. Sci. St. Péterb. 7 : 1–196.

Strauch, A. 1865. Die Verbreitung der Schildkröten über den Erdball. Mém. Acad. Imp. Sci. St. Péterb. 8 : 1–207.

Takara, T. 1969. Life and Nature of Ryukyus. Ryukyu Bunkyo Tosho, Naha. 206 p. (in Japanese)

Takashima, H. 1932. A list of turtles of the Japanese empire. Tr. Soc. Formosa. 22 : 152–163. (in Japanese)

Taylor, E. H. 1920. Philippine turtles. Philippine J. Sci. 16(2) : 111–144. +7 pls.

Tian, W., Y. Jiang, G. Wu, Q. Hu, E. Zhao and Q. Huang. 1986. A Checklist of Chinese Reptiles and Amphibians. Scientific Press, Beijing. 164 p. (in Chinese)

Toyama, M. 1985. The herpetology of the Ryukyu archipelago. *In*: W. W. F. Japan Scientific Committee (ed.), Conservation of the Nansei Shoto, Part 2. p. 54–152. World Wildlife Fund, Tokyo. (in Japanese)

Walbaum, J. J. 1785. Beschreibung der Spenglerischen Schildkröte. Schrif. Berlin Gesell. Naturf. Frende, 6 : 122–131.

Wermuth, H. and R. Mertens. 1977. Liste der rezenten Amphibien und Reptilien. Testudines, Crocodylia, Rhynchocephalia. Das Tierreich Lief. 28. Walter de Gruyter, Berlin. 174 p.

Zangerl, R. 1969. The turtle shell. *In*: C. Gans and T. S. Parsons (eds.), Biology of the Reptilia, Vol. 1. p. 311–339. Academic Press, New York.

Department of Zoology, Faculty of Science, Kyoto University, Kitashirakawa, Sakyo, Kyoto 606-01, JAPAN (YY, TH), Department of Biology, University of the Ryukyus, Nishihara, Okinawa, 903-01 JAPAN (HO)

要旨　スペングラーヤマガメとリュウキュウヤマガメの分類学的地位の再評価

安川雄一郎・太田英利・疋田　努

Geoemyda spengleri の2亜種，スペングラーヤマガメとリュウキュウヤマガメについて，多数の標本に基づく詳細な比較を初めて行った．その結果によれば，両者の間には著しい差異が存在しており，別種として扱うのが適当と思われる．また，近縁種との比較の結果は，両者が単系統群を構成することを示唆している．

（606-01 京都市左京区北白川追分町　京都大学理学部動物学教室（安川・疋田）・903-01 沖縄県中頭郡西原町千原1　琉球大学理学部生物学科（太田））