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Identity of the black soft-shell turtle *Aspideretes nigricans* (ANDERSON, 1875), with remarks on related species (Reptilia: Testudines: Trionychidae)

With 20 Figures

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Translation: JARMO PERÄLÄ

Kurzfassung. **Zur Identität der Dunklen Weichschildkröte *Aspideretes nigricans* (ANDERSON, 1875), mit Bemerkungen zu verwandten Arten (Reptilia: Testudines: Trionychidae).** – Die ontogenetischen Entwicklungsstadien der Dunklen Weichschildkröte, *Aspideretes nigricans*, werden detailliert dargestellt, diagnostische Merkmale herausgearbeitet und mit den ähnlichen Arten *A. gangeticus*, *A. hurum*, *A. leithii*, *Amyda cartilaginea* und *Nilssonia formosa* verglichen. *Aspideretes nigricans* war bislang nur aus dem Moscheeteich von Chittagong (Bangladesch) und umliegenden Tümpeln bekannt. *A. nigricans* wird in der vorliegenden Arbeit erstmals für den indischen Bundesstaat Assam nachgewiesen und damit als wildlebende Art identifiziert. Es werden detaillierte Fundortnachweise veröffentlicht und in einer Karte zusammengefasst. Beobachtungen zur Ökologie und zum Verhalten von *A. nigricans* werden vorgestellt. Des weiteren werden die phylogenetischen Beziehungen der Art und ihr Gefährdungs- und Schutzstatus diskutiert. *A. nigricans* scheint im Brahmaputra-Flusssystem in Assam weit verbreitet zu sein. In Teilen des Flusssystems existieren noch gute Populationsdichten. In Assam kommt *A. nigricans* syntop mit zwei weiteren *Aspideretes*-Arten vor (*A. gangeticus*, *A. hurum*). Um künftig die Artbestimmung zu erleichtern, wird ein auf externmorphologischen Merkmalen basierender Bestimmungsschlüssel für alle *Aspideretes*-Spezies sowie für *Amyda cartilaginea* und *Nilssonia formosa* vorgelegt.

Abstract. The ontogenetic stages of the black soft-shell turtle *Aspideretes nigricans* are presented in detail. Its diagnostic characteristics are pointed out and compared with the similar species *A. gangeticus*, *A. hurum*, *A. leithii*, *Amyda cartilaginea,* and *Nilssonia formosa*. Hitherto *Aspideretes nigricans* was known only from the Mosque water tank and nearby ditches in Chittagong, Bangladesh. In the present study *A. nigricans* is recorded for the first time for the Indian state Assam and identified as a wild-living species. Detailed locality records are provided and summarised in a map. Observations on ecology and behaviour of *A. nigricans* are presented. Its phylogenetic relationships, vulnerability and conservation are discussed. *A.*

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nigricans seems to be widely dispersed in the Brahmaputra river system in Assam. Good population densities still exist in parts of the river system. In Assam, *A. nigricans* occurs syntopically with two other *Aspideretes* species (*A. gangeticus*, *A. hurum*). To make future species determinations easier, a key for the species of the genus *Aspideretes*, *Amyda cartilaginea* and *Nilssonia formosa* is given, based on external morphology.

Key words. Reptilia, Testudines, Trionychidae, *Amyda cartilaginea*, *Aspideretes gangeticus*, *A. hurum*, *A. leithii*, *A. nigricans*, *Nilssonia formosa*, taxonomy, morphology, ontogeny, coloration, behaviour, distribution, status, conservation, Bangladesh, India, Assam.

Prologue

The black soft-shell turtle *Aspideretes nigricans* (ANDERSON, 1875), with a reputation of being a true rarity as the species is known exclusively from the tank at the shrine of Sultan al-Arefin Hazrat Bayazid Bistami in Chittagong, was studied exhaustively by M. F. AHSAN and co-workers (AHSAN & HAQUE 1987, AHSAN et al. 1991, AHSAN & SAEED 1992, AHSAN et al. 1994) but without clarifying the question of the origin of the species. AHSAN & SAEED (1989) even speculate: "Apparently the species has never existed in the wild state, but a semi-captive colony has become established in an enclosed pond of the shrine of Hazrat Sultan Bayazid Bistami of Chittagong".

If the turtle in question is a "domesticated" form or a subspecies of a known species, then a wild form would have to exist! While scientific explanations are lacking, various legends are quoted in recent literature in an attempt to explain the origin of the turtles in the tank of Chittagong. These legends rely upon a high degree of speculation. AHSAN & SAEED (1989) present in their work an abbreviated history of the shrine of Bayazid Bistami. According to one of these legends, Sultan al-Arefin Hazrat Bayazid Bistami from Bistam in Iran brought the founding stock of these soft-shell turtles into Chittagong in the 9th century A. D. If this were true, then the genus *Aspideretes* would show a disjunct distribution and the "ancestral form" of *A. nigricans* would live, or would have lived in historical times, undetected, somewhere in the Middle East!

Today, the "holy" turtles of Chittagong are not only regionally or nationally renowned (KHAN 1980, HONEGGER 1982, OBST 1985), but are also being promoted internationally as a tourist attraction, being mentioned in many travel guides (SANTIAGO 1985). Their popularity is accordingly high. Daily masses of travellers and pilgrims visit the holy site. AHSAN et al. (1994) write about notable quantities of bread, bananas and meat scraps sold as food for the soft-shell turtles. According to personal observation, women scoop water from the carapaces of the big, tame animals which come to the sides of the tank, and drink it in the hope of ensuring numerous descendants (PRASCHAG 1992).

Another pond inhabited by soft-shell turtles is located on the premises of the Kamakshya Temple at Gauhati in Assam, an important place of pilgrimage. When, according to Hinduist belief, one of the breasts of Goddess Kali plunged upstream and created the world's largest riverine island, Majoli, her pudenda (Yoni) landed at Gauhati and formed the area of Nilachal Hill. The Kamakshya Temple complex is primarily dedicated to the forces of creation. Here, Kali and her pudenda are being hailed as the highest creative principle and the overwhelming sexual abilities of the God Shiva are being praised. Tantrists have appeared here since centuries. The adjacent temple pond is consecrated to Shiva (NUGENT 1993).

1. Introduction

In the 19th century often only few specimens were available to zoologists for comparison, and many new taxa were described only on a meagre basis of material. This is especially true for large-sized soft-shell turtles. The material consisted primarily of osteological specimens

(skulls and shells) as well as alcohol preserved juveniles. Colour and shape characteristics for individuals depicted on colour plates were readily comprehended in the majority of cases. However, post-fetal ontogenetic changes of these features remained frequently unclear. This has lead to confusion with regard to similar taxa. It also explains the disproportionate number of conflicting interpretations based on one and the same species which have yielded different taxonomic results (see and compare synonymy lists in BOULENGER 1889, WERMUTH & MERTENS 1961, 1977, ZHAO & ADLER 1993).

Already GRAY (1872) pointed out, as simple as it is to identify a soft-shell turtle as such, so it is hard to classify one by species. The distinctiveness of superficial structures and colour characteristics as well as osteological features can change drastically during ontogeny in trionychids. In addition, the timing of final differentiation of these characteristics is prone to intraspecific variation.

As soft-shell turtles may reach a considerable age (e. g., over 50 years for *Trionyx triunguis*, SLAVENS & SLAVENS 2000: 145), they go through major alterations of form and stature in combination with changes in pattern and coloration during their life. Therefore, classification into species of very old individuals, especially of some Asiatic soft-shell turtles, poses great problems. Only after comprehension of the changes that occur during ontogeny in *Aspideretes* and closely related taxa is it possible to define a species to such a degree that confusion with other species can be excluded.

In addition, we have the uncommon situation that at least two nominal Southeast Asian soft-shell turtle species are based on animals living in temple ponds and are not known from the wild at all. Specimens derived from a stock subjected to living in such unnatural conditions on a long-term basis can show considerable morphological deviation in comparison with conspecifics from the wild, and are occasionally hard to identify. Reasons for their divergent appearance include unnatural food, strongly eutrophic water, a high stock density, inadequate opportunities for oviposition, as well as behavioural disorders due to constant harassment by humans. Further factors include frequently encountered bite wounds, injury-related and other deformities, fungal and parasite-induced infections, slime and algal growth, and natural age-related melanism. Juveniles are hardly known because of missing or limited reproduction.

The two species described exclusively from temple tanks are: (1) *Trionyx sulcifrons* ANNANDALE, 1915, which is regarded a synonym of *Aspideretes leithii* (GRAY, 1872) since SMITH (1931) and known only from the Jumma pond in Nagpur, NE Maharashtra (ANNANDALE 1915), and (2) *Trionyx nigricans* ANDERSON, 1875, considered valid (as *A. nigricans*) and hitherto known from the Chittagong shrine tank only. *Trionyx gangeticus mahanaddicus* ANNANDALE, 1912 from the temple pond in Cuttack (and Puri), Orissa, has also been reported from other regions and was synonymised with *Trionyx gangeticus* CUVIER, 1825 = *Aspideretes gangeticus* by SMITH (1931). Despite an account by VIJAYA (1983) about *A. leithii* in a temple pond at Kotipalli (Kondapalle) on the Krishna River in Andra Pradesh, where the animals are being fed hibiscus blossoms and bananas, and *A. leithii* shells collected at Godavari by fishermen, comparative studies to clarify the systematic status of *T. sulcifrons* and *T. gangeticus mahanaddicus* are still lacking. Until such studies are made, treating these names as junior synonyms of *Aspideretes leithii* and *A. gangeticus*, respectively, must be considered mere convenience.

Since the revision by MEYLAN (1987), the following four soft-shell turtles from the Indian subcontinent are assigned to the genus *Aspideretes*: Indian soft-shell turtle, *A. gangeticus* (CUVIER, 1825); Indian peacock soft-shell turtle, *A. hurum* (GRAY, 1830); Leith's soft-shell turtle, *A. leithii* (GRAY, 1872); and black soft-shell turtle, *A. nigricans* (ANDERSON, 1875).

All four species posses a similar appearance and feature, at least in the juvenile stage, a pattern of four to six ocelli on the carapace. An important osteological character shared by these species is the presence of two neurals between the first pair of pleurals (instead of one neural as in the remaining representatives of the tribe Trionychini sensu MEYLAN 1987).

The strong morphological similarities in coloration (of the ocelli), size, skull and shell shape among the four *Aspideretes* species extend also to the Burmese peacock soft-shell turtle, *Nilssonia formosa* (GRAY, 1869) and the Asiatic soft-shell turtle, *Amyda cartilagi-*

nea (BODDAERT, 1770). For this reason, we compare in the following the *Aspideretes* species with these taxa, too.
Hatchlings of the black soft-shell turtle are approximately 4.5 cm long (AHSAN et al. 1991); adult females attain a carapace length of 74 cm and adult males up to 91 cm (DAS 1995), with a mass of over 50 kg (AHSAN & SAEED 1989). At least the literary sources below include accounts of the following developmental stages of *A. nigricans*: Pattern and coloration of juveniles are described by AHSAN et al. (1991); a colour illustration is presented in PRASCHAG (1992). The remaining descriptions are based on coloration of adult or extremely old animals (e. g., ANDERSON 1875, ANNANDALE 1912). PRITCHARD (1979) compares between these two slightly divergent accounts of the late 19th and early 20th century. Further descriptions of adults are found in AHSAN et al. (1994), ANNANDALE & SHASTRI (1914), DAS (1991, 1995) and RASHID & SWINGLAND (1997). Accounts of intermediate, medium-sized, specimens are missing, with one exception (ANNANDALE & SHASTRI 1914).
During this study, numerous specimens of soft-shell turtles from Southeast Asia were investigated with a focus on coloration, pattern, and shape of shell and skull at various ontogenetic stages. Therefore it was for the first time possible to verify the existence of black soft-shell turtles in the wild in Assam. To make identification of Southeast Asian soft-shell turtles easier in future, a key is presented here for *Amyda*, *Aspideretes* species, and *Nilssonia formosa* based on external characters.

2. Materials and Methods

Abbreviations: The Natural History Museum London (BMNH), Naturhistorisches Museum Wien (NMW), alcohol preparations (A), dry preparations (D).

Museum material examined
Amyda cartilaginea: BMNH 68.5.18.2 (Araccan Range, W. of Pegu, Coll.: W. Theobald, skull, ad., D, type of *Trionyx phayrei* THEOBALD, 1870), BMNH 87.8.6.1 (Araccan Range, W of Pegu, Coll.: W. Theobald, pres. by Council of Bristol Museum, shell, ad., A, type of *Trionyx phayrei* THEOBALD, 1870), NMW 160 (Bogor, Buitenzorg, Java, Adensamer 1907, 1 skull with 2 horny plates [alveolar surfaces of the mandible], ad., D), NMW 1301 (Cochinchina, S Vietnam, 1 carapace, ad., D), NMW 1863 (Amanvit Fluß, Borneo, Grabowsky 1882, Siebenrock collection, 1 mounted skeleton, ad., D), NMW 1864 (Pagatan, Palat, Borneo, Grabowsky, 1882, Siebenrock collection, 1 mounted skeleton, ad., D), NMW 1873 (Bogor, Buitenzorg, Java, Umlauff, Hamburg, don. Steindachner 13.4.1899, Siebenrock collection, 1 mounted skeleton, juv., D), NMW 1874 (Bogor, Buitenzorg, Java, Adensamer, 1907, Siebenrock collection, 1 mounted skeleton, juv., D).

Aspideretes gangeticus: BMNH 48.2.1.38 ("India", Pres.: Capt. Boyes, subad., D), BMNH 48.2.1.41 (Sulranpoor, Pres.: Capt. Boyes, skull, D), BMNH 80.1.28.9 ("India", Coll.: R. McClelland [Purch.: Indian Museum], shell, ad., D), BMNH 80.1.28.10 ("India", Coll.: R. McClelland [Purch.: Indian Museum], shell, ad., D), BMNH 86.8.26.1 (Calcutta, ad., skeleton, D), NMW 1300 (Indien, ad., D), NMW 30221: 7 ("Asien", juv., don. Weissinger, A), NMW 30235: 2-3 (Pakistan 1971, Sochurek imp. et don., juv., A), NMW 30265: 1-5 (Pakistan, Sochurek don., 1972/32, juv., A), NMW 30266 ("Singapore", im Tausch v. Museum Triest, 1881, subad., A), NMW 30678 (Tiergarten Schönbrunn, 10.09.1986, subad., A), NMW 33216: 1, 2 (Pakistan, Nachlass Weissinger 1993, juv., A).

Aspideretes hurum: BMNH 1973.1051 ("India", Pres.: Gen. Hardwicke, juv., A, probably syntype of *T. sewaare* GRAY, 1872), BMNH 1973.1052 ("India", Pres.: Gen. Hardwicke, juv., A, probably syntype of *T. sewaare* GRAY, 1872), BMNH 1973.1053 ("India", Purch.: Mr. Stevens, juv., A), BMNH 1973.1054 ("India", Purch.: Mr. Stevens, juv., A), BMNH 1973.1055 ("India", Purch.: Mr. Stevens, juv., A), BMNH 51.5.9.1 (Purch.: Mr. Argent, juv., A), BMNH 68.2.12.15

("India", Pres.: Mr. Charles Falconer, skull, ad., D), BMNH 81.7.8.4 ("Bengal", Pres.: W. Theobald, skull, D), BMNH 86.8.26.2 (Calcutta, Purch.: E. Gerrard jr., ad., D), NMW 30235: 4, 5 (Pakistan 1971, Sochurek imp. et don., juv., A), NMW 31269: 1-8 (Bayder Bazar near Sonargaon, 30 km SE Dacca, Bangladesh, don. Gemel 9/1987, shell parts, subad., D).

Aspideretes leithii: BMNH 1869.8.28.10 (Poonah, Pres.: Dr. Leith, subad., D, type), BMNH 1870.7.11.1 (Poonah, Pres.: Dr. Leith, subad., D, type), BMNH 1884.3.25.1 (Pres.: G. E. Mason, juv., A), BMNH 1884.3.25.2 (Pres.: G. E. Mason, juv., A), BMNH 1908.12.28.20 (River Kistna, Pres.: Dr. Dobson, A. M. College, juv., A), NMW 30202 (Indien, 1839.V.53a, juv., A), NMW 30234 (Birma, Indien, Rev. A. Eden, Mus. Kalkutta im Tausch 1909.6, juv., A).

Aspideretes nigricans: BMNH 1929.12.23.1 (Chittagong tank, E Bengal, Pres.: Indian Museum, ad., skeleton, D), BMNH 1929.12.23.2 (skull of BMNH 1929.12.23.1, D), BMNH 1994.449 (Nazira, north of the Naga Hills, Eastern Assam, India, Coll.: J. M. Foster, Pres.: M. A. Smith, juv., A), 4 live specimens in care of the first author, import permit 207/000/903804/01/9 (23.11.1999).

Nilssonia formosa: BMNH 68.4.3.142 (Pegu, Coll.: W. Theobald, juv., A, type of *Trionyx peguensis* GRAY, 1870), BMNH 68.4.3.143 (Pegu, Coll.: W. Theobald, juv., A, type of *Trionyx peguensis* GRAY, 1870), BMNH RR1946.1.22.10 (Pegu, Coll.: W. Theobald, skull, juv., A, type of *Trionyx peguensis* GRAY, 1870), BMNH RR1946.1.22.11 (Pegu, Coll.: W. Theobald, skull, juv., A, type of *Trionyx peguensis* GRAY, 1870), NMW 30235: 1 (Burma, 02.05.1869, Coll. Stoliczka, juv., A), 2 live specimens in care of the first author.

Data collected in the field

In 1997, during a trip to Bangladesh and Myanmar, the first author studied large numbers of soft-shell turtles at turtle wholesalers in and around Dhaka, Bangladesh. In Myanmar temple tanks of the Botataung Pagoda and the Shwe-Dagon-Pagoda in Yangon (Rangoon) and the pond facing the Maha Myat Muni Buddhist Temple in Mandalay were surveyed. Soft-shell turtles were found to be traded sporadically from concealed containers at the market place of Bago (former Pegu). Among salesmen in Yangon, Pyu, Taungoo and at Lake Inle the opportunity arose to examine *Amyda cartilaginea* and *Nilssonia formosa* in more detail.

In November 1998, February 1999 and October/November 1999 the first author travelled through northeastern India to collect further data on chelonians (see also PRASCHAG & FACHBACH 2001). Nameri National Park, Kaziranga National Park, Dibru Saik-howa Wildlife Sanctury and Orang Wildlife Sanctuary, in addition to fishing villages and Assam's most important fish markets such as Gauhati, Nowgong, Tezpur, Bishwanath, Jorhat, Sibsagar, Dibrugarh, Tinsukia, Golaghat and Hojai were visited. With the help of colour photographs, fishermen and locals along the Brahmaputra and its tributaries were interviewed about the turtle fauna and its utilisation. All turtles captured (1 *Aspideretes gangeticus*, 6 *A. hurum,* and 6 *A. nigricans*) were measured and photographed. Temple ponds inhabited by turtles were monitored repeatedly.

The second author made journeys to both Bangladesh and India in February 1987 and 1991, and on both occasions visited the *A. nigricans* at the mosque water tank in Chittagong. The turtles and their feeding were carefully observed and photographed. The mosque's administration provided additional information. In 1987 a local boy succeeded in catching a shy, half-grown turtle from a muddy pond approximately 200 m from the mosque tank with the mosque's administrators' permission. This animal was photographed and released. In 1991 video recordings were made of the feeding of the large black soft-shell turtles in the shrine tank. Also in 1991, courtesy of Prof. B. A. BHUIYA of the Zoological Institute in Chittagong, we photographed the preserved hatchlings of *A. nigricans* kept at the institute (PRASCHAG 1992).

Visits to turtle traffic middlemen in Baiyder Bazar and Sonargaon, Bangladesh in 1987, and to two wholesalers in Dhaka in 1991, enabled the second author to survey large numbers of

live soft-shell turtles and to get acquainted with their variability. These soft-shell turtles were destined for the international food trade. Several hundred hatchlings to three-year old juveniles of *A. hurum* and *A. gangeticus* were observed at head-starting centres in Morena, Kukrail and Varanasi, among other turtle species.

Methods

Locality co-ordinates in the field were ascertained using GPS 12 (Garmin).
Four live juveniles of *A. nigricans* from the holdings of the first author (P. P.) were x-rayed, and genus and species-specific osteological characters were copied from a radiograph onto a drawing on a light table using a transparency sheet.

3. Results

3.1. Morphology of *Aspideretes nigricans*

Skull

All four live *A. nigricans* and the skull BMNH 1929.12.23.2 show in the lower jaw a distinct bony crest inside the cavity of the mandibular symphysis. This character is easily recognisable in an open jaw (Fig. 1). The width of the mandibular symphysis equals the diameter of the eye in both juveniles and adults.

Carapace

Radiographs derived from two out of four live turtles (live specimens 1 and 2) could be used for evaluation of the configuration of neurals (Fig. 2): According to our findings, both animals show two neurals (or one preneural and one neural) between the first pair of pleurals, which proves that the specimens are attributable to the genus *Aspideretes*. Specimen number 1 (Fig. 2 A) has the neural reversal between 5th and 6th, specimen 2 between 6th and 7th (Fig. 2 B), both on a quadrilateral diaphragm neural. Conditioned by the divergent morphogenesis of the nuchal from the rest of the bony disc (= bony carapace consisting of neurals and pleurals only; terminology sensu MEYLAN 1987: 13), and because these are juvenile animals, a gap occurs in a radiograph between the nuchal and the rest of the bony carapace. (The nuchal is not yet fused to and does not even touch the first neural and the first pair of pleurals). Thus the nuchal appears as an isolated element. Specimen number 2 (Fig. 2 B) shows a beginning development of the anterior and posterior costiform process of the nuchal. Both specimens exhibit nine neuralia.

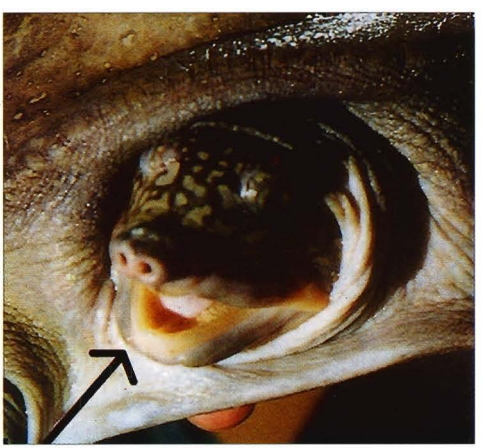

Fig. 1: Lower jaw symphysis of *Aspideretes nigricans*, live specimen no. 1. Photo: P. PRASCHAG

In (very) old animals, because of relatively longer 6th through 8th pleural pairs the bony disc retains in its posterior part a rectangular outline. This condition is recognisable in a live animal (with fully developed cartilaginous margin) as well as in dry preparations and in the bony disc BMNH 1929. 12.23.1. This shape is more pronounced in males than in females and juveniles.

Plastron

The radiograph of the live specimen number 1 shows the following findings (Fig. 3 A): Epiplastra separated from one another, their shanks approximately equally long proximally and distally, entoplastron moderately obtuse-angled. The medial processi of the hypoplastra are caudally oriented and

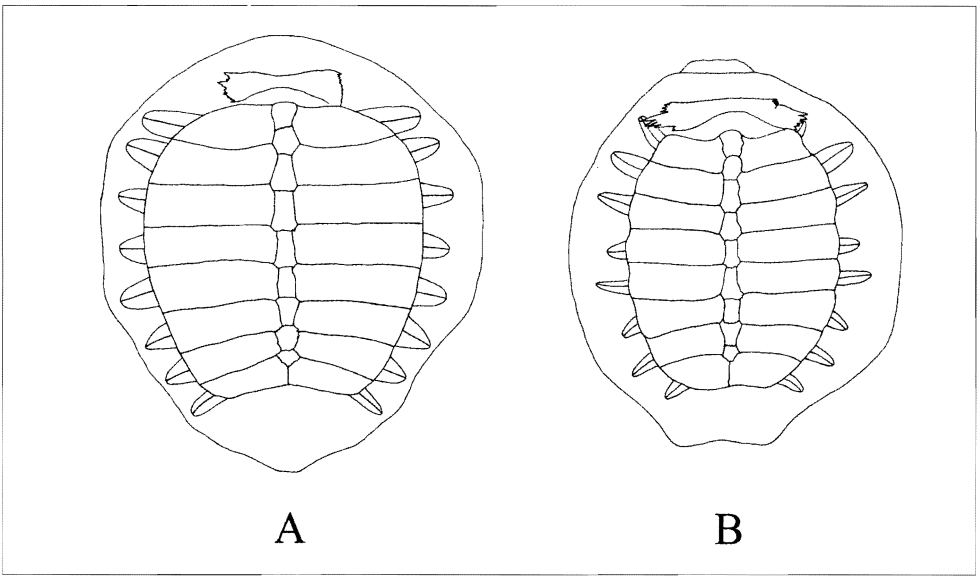

Fig. 2: Carapace of *Aspideretes nigricans* with neural configuration of A: Specimen 1, B: Specimen 2. Bony disc with outline of shell. Redrawn from radiographs. Illustration: R. GEMEL

therefore form a greater cranially oriented, and a smaller caudally oriented, fenestra. The xiphiplastra are elongated.
The epiplastra of an adult specimen BMNH 1929.12.23.1 (Fig. 3 B) are in contact with one another at the bend, diverge distally to form relatively long shanks and produce a pronounced cranial crest on the anterior lobe. The entoplastron is remarkably obtuse-angled and it exhibits intense fusion with the epiplastra. An entoplastral callosity is distinctly developed. Because of the particular form of the entoplastron, the opening between entoplastron and hyo-hypoplastron is reduced to a narrow split and the base of the anterior plastron lobe stretches in the adult specimen close to the bony middle portion of the hyo-hypoplastron. Perhaps this split is the result of preparation and in life the entoplastron is in close contact with the hyoplastra.

3.2. Pattern and coloration, and ontogenetic change in *Aspideretes nigricans*

All trionychids are capable of hormonally induced physiological change in colour intensity (BARTLEY 1971). The limits of this change in *Aspideretes nigricans* vary between pale olive-green and blackish-dark grey, and this phenomenon is highly dependent on the background or the environment. Yet there are clear ontogenetic changes. The alterations in pattern and colour during post-fetal ontogeny are markedly stronger in *A. nigricans* than in the three other *Aspideretes* species. The changes in coloration and stature can be classified into several phases with overlapping continuity:

Phase 1: From hatchling to 10-15 cm carapace length (Figs. 4.1.1., 4.1.2., 5.1.)
The basic colour of the nearly circular carapace is dark olive-brown with numerous larger and smaller, substantially paler, olive-brown flecks. There are four (exceptionally probably also five or six) distinct ocelli, as found in juvenile *Aspideretes hurum* and *Nilssonia formosa*. Each ocellus consists of four concentric rings (AHSAN et al. 1991). The centre is black and is surrounded by a thin, sharply delimited orange-coloured ring. The third ring is dark grey to almost black and three to four times broader than the preceding one, but has equally circular,

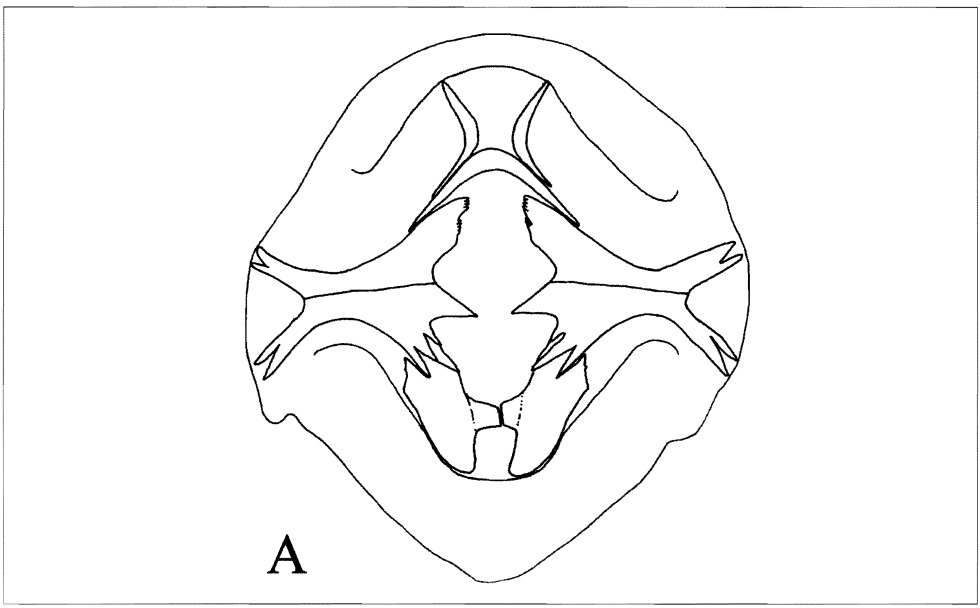

Fig. 3: Plastron of *Aspideretes nigricans*. A: Specimen 1, redrawn from radiograph. Illustration: R. GEMEL

well delimited borders. The last ring has exactly the same olive-grey colour as the pale flecks on the carapace, and is at least as wide as the preceding ring, usually very slightly wider. The outermost borders are not so regularly round as the other rings. The dark olive-grey to brown ground colour of the carapace touches this olive-grey ring. Because the paler olive-grey flecks usually do not fuse with the equally coloured fourth ring, and because these flecks are often located at regular intervals from the last ring, this gives an impression of a fifth ring.

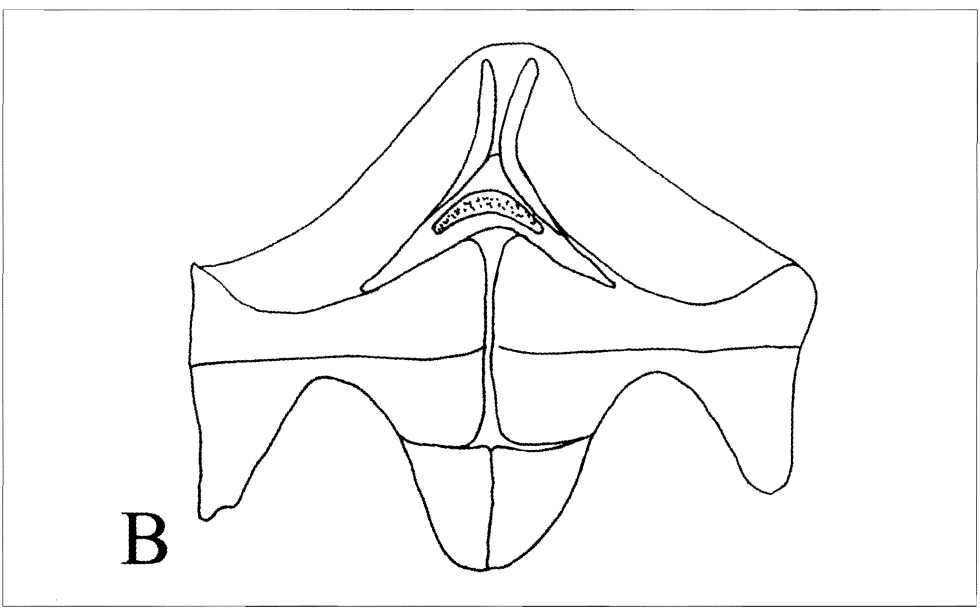

Fig. 3: Plastron of *Aspideretes nigricans*. B: BMNH 1929.12.23.1. Illustration: R. GEMEL

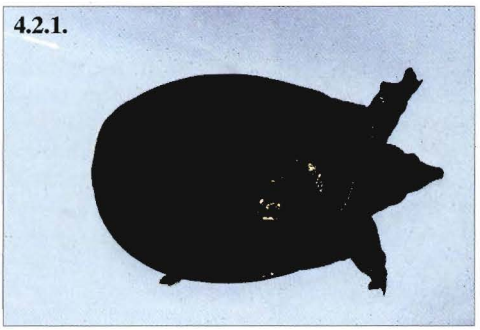

Fig. 4: Overall appearance and coloration of *Aspideretes nigricans* in the course of ontogenetic development. **4.1.: Phase 1:** 4.1.1.: Hatchling from Chittagong, 4.1.2.: Juvenile, CL = 6 cm, Nameri National Park; **4.2.: Phase 2:** 4.2.1.: Fading out of Phase 1, beginning of Phase 2, CL = 14.5 cm, Kamakshya, 4.2.2.: Phase 2: CL = 20 cm, Kamakshya; **4.3.: Phase 3:** Nagsankar; **4.4.: Phase 4:** Chittagong. Photos: 4.1.1. and 4.4.: R. GEMEL, all other photos: P. PRASCHAG

The skin above the bony disc features longitudinal rows of elongated tubercles. Irregularly scattered tubercles occur in moderate amounts on the posterior carapace rim. Nuchally, a row of 15 to 20 very large, fully developed longitudinal tubercles are found. The outer rim of the carapace, excluding the cranial region, is yellow to orange, and sharply distinct from the basic coloration. A zone in which the dark olive-grey to brown ground colour is interspersed with numerous yellowish dots is attached to this yellow-orange ring in its lateral and caudal regions. The paler olive-grey flecks do not penetrate inside this zone. The plastron of very small specimens is dark grey to black with small yellow dots which can be so tiny and dense that the plastron receives a metallic sheen.

The basic colour of the head (Figs. 4.1.1., 4.1.2.) is equally dark grey to black. A distinct grey to dirty-yellow band runs diagonally over the base of the proboscis. A large postorbital fleck of grey to yellowish colour and more or less triangular shape is located immediately behind the eye.

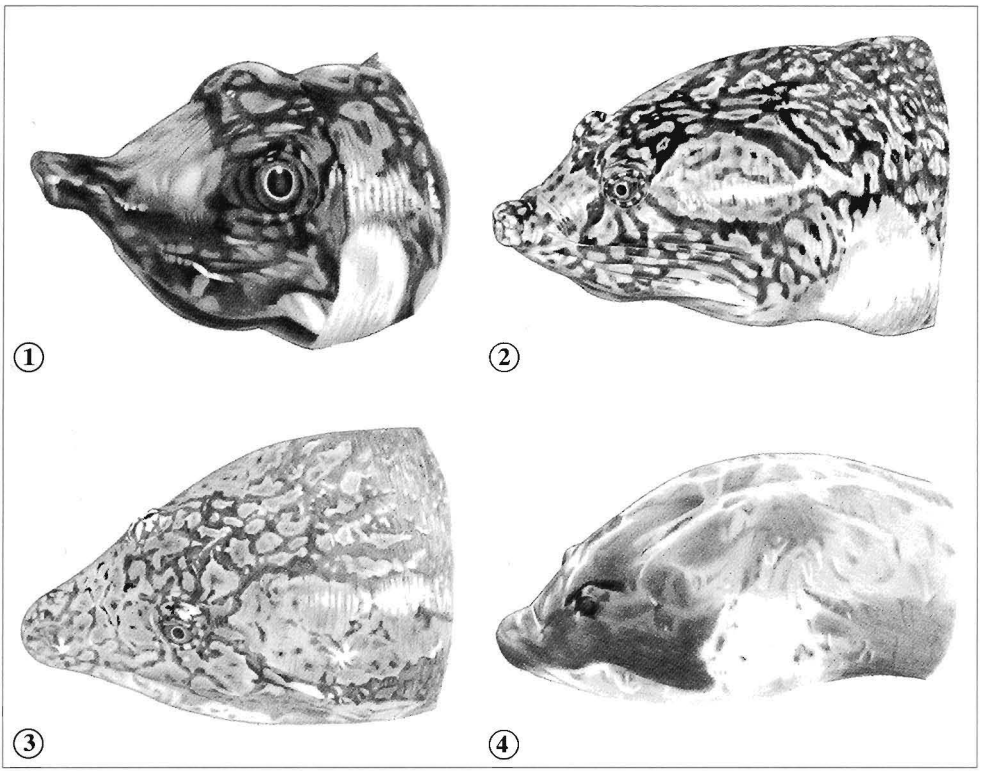

Fig. 5: Head pattern of *Aspideretes nigricans* during ontogeny. 1 to 4 correspond to Phases 1 to 4 (for explanations, see text). Illustration: G. URBANEK

The lateral parts of the head feature an even larger distinct and characteristically shaped temporal fleck which is yellow in very small specimens, but which fades rapidly with ensuing growth. The dorsal head surface is covered with larger dirty-yellow flecks. These flecks later become greenish, contributing to a vermiculated pattern. The fleshy upper lips are yellow in their posterior parts. With the eyes open, the eyelids are radiating zebra striped with alternating black and dirty-yellow coloration. Ventrally the colour of the plastron and soft parts on the extremities and tail is dark grey to black, speckled with numerous yellow dots and blotches. The yellow elements appear first creme-coloured in hatchlings, and they go through a transformation into a greyish green with ensuing growth.

Phase 2: Juveniles of about 15 to 45 cm carapace length (Figs. 4.2.1., 4.2.2., 5.2.) The already elongated carapace has a dark olive-grey, mostly olive-brown, ground colour. The paler flecks of younger individuals appear turbidly indistinct, and they cross over into the darker ground colour. The ocelli are now only hinted at and are visible as slightly darker flecks with an insignificantly paler centre. The carapace is sprinkled with yellow dots and speckles contributing to a similarity with *Amyda cartilaginea* (Fig. 6) and *Rafetus euphraticus* (DAUDIN, 1802). The tubercles arranged in longitudinal rows have disappeared. The plastron is pale grey, the yellow dots faded or already indistinguishable. The head has a dark brown to black ground colour with olive-green markings. The band at the base of the proboscis gradually fades out (Fig. 5.2): At first dark flecks appear in the middle of the olive-green band so that relative to the ground colour, the initially rectilinear borders rupture until this paedomorphic feature is dissolved into the surroundings. The postorbital fleck is olive-green and still distinct. However, this fleck, too, starts to dissolve slowly. The large

temporal fleck also loses its rectilinear demarcation relative to the ground colour of the head, and gradually becomes whitish or even white in the lower region. The posterior region of the fleshy upper lips is pale grey to whitish. The eyelids, when open, feature a distinct black and olive-green zebra pattern. An arrangement of olive-green flecks is found on the upper head region. The dorsal surfaces of the extremities are olive-green to dark grey studded with pale dots. The respective ventral surfaces are pale brown. The remaining soft parts are coloured uniformly grey, olive-green to brownish, and exhibit only faded yellow dots, if at all. The skin between neck and anterior extremities is somewhat wrinkled.

Fig. 6: *Amyda cartilaginea* on the market in Bago (Pegu), Myanmar. Photo: P. PRASCHAG

Phase 3: Young adults, from about 45 cm carapace length onwards (Fig. 4.3., 5.3.)
The oval carapace is uniformly coloured grey, olive-green copper (ANNANDALE & SHASTRI 1914), brown or lightly marbled. The ocelli have completely disappeared. The plastron is dark grey. The already massive head has a dark olive-green to dark grey ground colour, occasionally with a grey-blue shimmer. The head appears to be blunter now, and the proboscis is extended in a lesser degree (Fig. 5.3.). The vermiculated markings of the head are marbled. The band at the base of the proboscis is fully obscured by the dominant pigmentation. The postorbital flecks are still partly visible but no longer well separated from the remaining head markings. The whitish temporal fleck expands with age and is now distinct from its surroundings. The posterior region of the upper lip is white. Soft parts and extremities, neck and ventral surfaces are olive-green to dark grey. Large warts have developed between neck and anterior extremities.

Phase 4: Adults (Fig. 4.4., 5.4.)
The carapace is olive to dark grey, usually without any markings. We were unable to detect a longitudinal median furrow in the posterior part of the carapace (ANDERSON 1875, ANNANDALE & SHASTRI 1914, AHSAN et al. 1994). The coloration of the plastron is dark grey with a blackish glitter. The head is coloured olive-green or brownish, and it has broadened massively due to the wide jugal arches for the strongly hypertrophied jaw adductors. The blunt head narrows uniformly towards the anterior, the proboscis is hardly exposed (Fig. 5.4.). A fine vermiculation extending from the apex of the proboscis to just behind the eyes is detectable. The temporal fleck is snow-white and thus is the most prominent component of the pattern. The posterior two thirds of the upper lip are also white. Additionally, some specimens feature a white fleck in wrinkled regions of warts between neck and anterior extremities.

Diagnostic Differences

Because of pronounced morphological similarities between *Aspideretes nigricans* and the remaining soft-shell turtles dealt with here, important diagnostic differences for various size classes are provided as follows (*Aspideretes leithii* can be disregarded because of its distant distribution).

Phase 1

Aspideretes hurum closely resembles *A. nigricans*. However, the postorbital and temporal flecks are markedly smaller in *A. hurum*. The top of the head, especially the region between the eyes, appears unicoloured and sprinkled with small dots and flecks. In *A. nigricans*, the top of the head is covered by substantially bigger flecks contributing to a net-like, reticulated pattern.
Juveniles of *A. gangeticus* are differentiated by their uniformly olive-green to grey carapace. The ocelli are comparatively inconspicuous, without yellow or orange coloration between the dark concentric rings. During this phase in this very variable species, in animals from Assam, and relative to the grey ground colour, the clearly demarcated black stripes on the head are well differentiated. The top of the head is characteristically olive-green coloured.
Nilssonia formosa shows two very small and most often round yellow to orange postorbital flecks. The temporal flecks stretch far up to the top of the head, almost touching one another sagittally. The band at the base of the proboscis is absent.

Fig. 7: *Aspideretes hurum* with typical coloration on the market in Nowgong, Assam. Photo: P. PRASCHAG

Fig. 8: An animal resembling *Aspideretes hurum*, "*sewaare* morph" on the market of Nowgong, Assam. Photo: P. PRASCHAG

Phase 2

The yellowish-grey band at the base of the proboscis and the postorbital flecks are retained in *Aspideretes hurum* (Fig. 7, 8) whereas these markings disintegrate in *A. nigricans*. *A. hurum* features distinct ocelli. The carapace is not sprinkled with yellow.
The postorbital flecks are lost in *Nilssonia formosa*. The basic colour of the head is grey with dark flecks on the top of the head and an orange temporal region (Fig. 9).

Phase 3

Aspideretes gangeticus bears a pattern with distinct black head stripes, without zebra pattern on the eyelids and with no white temporal fleck (Fig. 10).

Phase 4

Aspideretes gangeticus lacks the prominent white flecks at the temporal region, and between neck and anterior extremities.

3.3. Size, weight, and sexual dimorphism in *Aspideretes nigricans*

Fig. 9: *Nilssonia formosa* on the market in Yangon (Rangoon), Myanmar. Photo: P. PRASCHAG

Fig. 10: *Aspideretes gangeticus* from Bishwanath, Assam. Photo: P. PRASCHAG

Among recent New World soft-shell turtles females grow larger than males. In contrast, in some Old World soft-shell turtles males attain a larger size than females, and this includes *Aspideretes nigricans* (AHSAN & SAEED 1989, DAS 1991, 1995). MEYLAN (1987: 14) considers this to represent an ancestral state. The carapace of females of *A. nigricans* is rounder than in males (AHSAN et al. 1994, in concordance with personal observations). Males have a more elongated shell and distinctly longer and thicker tails. Out of 100 specimens measured by AHSAN & SAEED (1989) at the mosque tank in Chittagong, the largest male had a carapace length of 78 cm (n = 54), the largest female of 74 cm (n = 46). However, the maximum length of males is 91 cm (DAS 1995). AHSAN & SAEED (1989) found that most males had shell lengths between 64 and 78 cm, most females between 39 and 53 cm, the heaviest specimen weighed 54 kg. Fishermen at a small village on the northern bank of Brahmaputra told us *A. nigricans* weighs 30 to 35 kg on the average. The heaviest animal was 57 kg. In comparison, *A. gangeticus* is able to reach a mass of up to 70 kg whereas *A. hurum* is considerable smaller and lighter, with an average weight of only 15 to 20 kg. These fishermen have specialised in catching freshwater turtles and harvest approximately one ton of turtles a week (!).

3.4. Distribution of *Aspideretes nigricans*

ANNANDALE (1912) presented a list of Indian soft-shell turtles, a supplement to BOULENGER's (1890) "Fauna of British India", with the additions of two subspecies, and *Trionyx nigricans*. The introduction includes a commentary about the distribution of this species: "It inhabits a tract of country intermediate between the Brahmaputra river-system and the

Arrakan streams in which a Burmo-Malay species of the genus first makes its appearance." This remark could indicate a larger range (AHSAN et al. 1991), however, with reference to the distribution data presented in conjunction with the description (ANNANDALE 1912: 165) it becomes clear that all specimens examined with one exception originate from the Chittagong tank (Fig. 11: Dot 1). This exception is a skeleton gathered in 1849 by ANDERSON in Calcutta. According to ANNANDALE (1912), the locality Calcutta must be ignored until an occurrence there is proven by a catch in the Ganges delta as *Trionyx nigricans* is an intermediate species between *Trionyx gangeticus* and *Trionyx phayrei* (*Amyda cartilaginea*, type locality: Hills of Arakkan) in distribution as well as structure. Indeed, the commercial trade in turtles for consumption was exorbitant in Calcutta during the 19th and 20th centuries, and until recently. Immense quantities of turtles, which were transported over hundreds or thousands of kilometres, landed on the fish markets of Calcutta (WEDEMAYER 1975, CHOUDHURY & BHUPATHY 1993). On these grounds, Calcutta should not be given much weight as a place of origin.

All evidence taken into account, the tank at the Chittagong mosque currently represents the sole known occurrence of *A. nigricans* (ANDERSON 1875, ANNANDALE 1912, ANNANDALE & SHASTRI

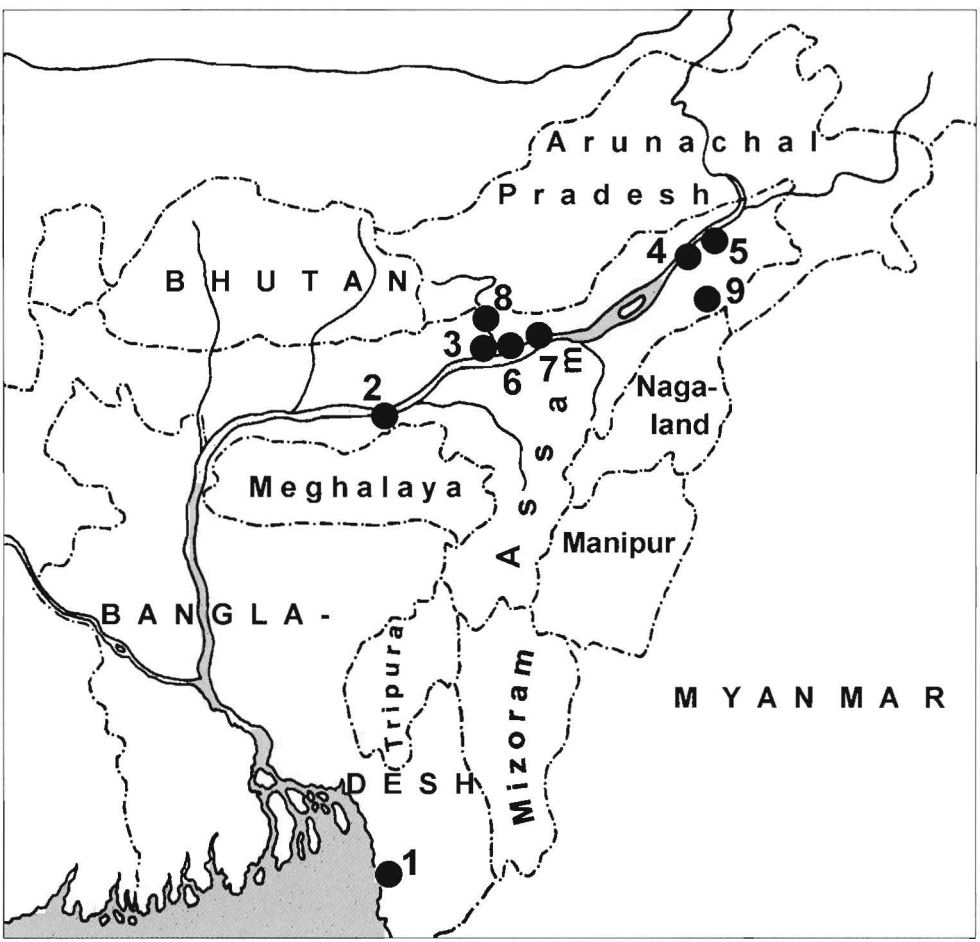

Fig. 11: Localities for *Aspideretes nigricans*. **Bangladesh: (1)** Chittagong, temple tank (type locality); **Assam, India: (2)** Kamakshya, temple pond; **(3)** Nagsankar, temple pond; **(4)** Dibrugarh; **(5)** Tinsukia; **(6)** Bis(wa)nat Ghat; **(7)** northern bank of the Brahmaputra on the opposite side of the Kaziranga National Park; **(8)** Nameri National Park; **(9)** Nazira (BMNH 1994.449). Illustration: U. FRITZ

Fig. 12: Mud puddle (ditch) located approx. 150 m from Chittagong temple pond; the locality for a semi-adult *Aspideretes nigricans*. Photo: R. GEMEL

1914, PRITCHARD 1979, KHAN 1980, 1982, HONEGGER 1982, OBST 1985, DAS 1989, ERNST & BARBOUR 1989, PRASCHAG 1992, FRAZIER & DAS 1994, ASIAN TURTLE TRADE WORKING GROUP 2000). Additional animals, most probably derived from the mosque pond population, could be found only in a nearby ditch (Fig. 12; RASHID 1990, DAS 1991, 1995) or ditches (KHAN 1987, AHSAN & SAEED 1989, AHSAN 1997, RASHID & KHAN 2000). These animals are mainly females, that probably left the temple tank in search for a suitable place to lay their eggs, and never found their way back (AHSAN & SAEED 1989). This ditch (mud puddle) was drained in the 1980s (DAS 1991). Until today, *A. nigricans* is not known from the wild, and the species is considered an endemic for Bangladesh. However, according to our observations *A. nigricans* is the most common species to be encountered in temple ponds inhabited by turtles in Assam. In all three tanks examined, the first author found black soft-shell turtles. Probably the best-known of the temple ponds in Assam, Kamakshya (Fig. 11: Dot 2, Fig. 13; 26°09.960' N 091°42.356' E), even contained exclusively *A. nigricans* (misidentified as *A. hurum* by DAS 1991, 1995). According to priests and locals, the soft-shell turtles reproduce here every year, and animals of every size are found. Although all of the water is changed occasionally, the first author witnessed the pond in an advanced eutrophic state at any time. However, the animals did not suffer from fungal infections, unlike their conspecifics in Chittagong. Nevertheless, many turtles feature healed bite wounds in the form of unpigmented regions or cuts in the carapace rim. Because of the escape of many animals in previous years, an obstruction was constructed around the banks.

The Nagsankar temple pond (Fig. 11: Dot 3) is located between Tezpur and Bish(wa)nath on the northern strand of Brahmaputra (26°43.518' N 92°59.682' E). This pond is surrounded by a large area of grassland. Beside a few specimens of *A. gangeticus*, here too the dominant species is *A. nigricans*.

The third temple pond, in which *A. nigricans* was observed, was visited in November 1998. This pond is approximately three car-driving hours east of Gauhati, on the southern bank of the Brahmaputra. Unfortunately no more detailed information about the location can be stated.

In February 1999, two semi-adult *A. nigricans* were for sale on the fish market in Dibrugarh. The fisherman who had caught the animals guaranteed the first author that he had fished both indi-

Fig. 13: *Aspideretes nigricans* during feeding time at Kamakshya temple pond, Assam; Phase 4. Photo: P. PRASCHAG

viduals from the Brahmaputra in the immediate vicinity of Dibrugarh (Fig. 11: Dot 4). *A. nigricans* is also well known to fishermen in Tinsukia (Fig. 11: Dot 5), northeast Assam.

In autumn 1999, an opportunity arose to measure and photograph a subadult male at fishermen near Bisnath Ghat (Fig. 11: Dot 6, Fig. 14), as well as a pair across the river at Kaziranga National Park (Fig. 11: Dot 7). All three animals were caught from the Brahmaputra. The first author caught by hand a 7 cm long juvenile in Nameri National Park (Fig. 11: Dot 8, Fig. 15), which continues as the Pakhui Sanctuary at the border with Arunachal Pradesh, in autumn 1998.

DATTA (1998) found in April 1996 in adjacent Pakhui Sanctuary (Arunachal Pradesh) two juvenile soft-shell turtles, which he identified as *A. hurum*. Judging by the description, these most likely represent *A. nigricans*: "Four very prominent large eye spots on carapace. Eye

Fig. 14: Biotope of wild *Aspideretes nigricans* in the Brahmaputra, vicinity of Bisnath. Photo: P. PRASCHAG

Fig. 15: Biotope in Nameri National Park, Assam. Locality for a living juvenile *Aspideretes nigricans*.
Photo: P. PRASCHAG

spot – black circle surrounded by orange yellow ring, the outer circle around the yellow ring also black. Whole body mottled, blotched pattern of ochre yellow brown rectangular patches, stripes and spots, dark brown to black background. Circular carapace. Plastron greyish. Head with black reticulations and yellow patches" (see key below).
According to the inference presented above, the black soft-shell turtle seems to be widely dispersed in the Brahmaputra river system in Assam. In contrast, the species could not be unquestionably identified from photographs by local fishermen in Silchar, south of the Cachar Range in southern Assam. Its occurrence in Arunachal Pradesh is probable, especially in the southeast. A possible distribution in Nagaland, Meghalaya, and in the wild in Bangladesh remains to be examined.
The fishermen of Assam discriminate between seven soft-shell turtle species living in the Brahmaputra. Two giant soft-shells are known to occur there: *Chitra indica* (GRAY, 1831), and *Pelochelys cantorii* (GRAY, 1864), the existence of which was not previously verified in Assam. BHUPATHY & CHOUDHURY (1992) question the occurrence of *C. indica* in Assam, but the first author was able to confirm its existence here in February 1999, based on five live specimens. Also two *Lissemys* taxa are known. Beside *Lissemys punctata andersoni* WEBB, 1980, yet another unmarked flap-shelled soft-shell taxon is supposed to occur here, too. The fishermen are well acquainted with three *Aspideretes* species. The most common species, *A. gangeticus*, is called Laumura or Laomora, and its occurrence in Assam was first recorded by BHUPATHY & CHOUDHURY (1992). *A. hurum*, which is locally called Teli-Gura, and *A. nigricans*, Gura, are considered close relatives, but most fishermen treat them as two separate forms. As *A. nigricans* has now been shown to occur in Assam, it has to be included in the list of Indian fauna.

3.5. Ecology and behaviour of *Aspideretes nigricans*

Because of the fortunate direct observation of a swimming juvenile in Nameri National Park (Fig. 15), which was subsequently caught, it is now possible to present first-hand descriptions of the habi-

tat: The area is flooded by the dense river system of the Jia-Bhoroli, which finally runs into the Brahmaputra, and contributes to its tributaries. The river water is so clear at the peak of the dry season that the structure of the river bottom is still visible in 1.5 m deep water. Due to correlated factors such as fast water flow, high oxygen contents, and low water temperature, the fish fauna differs greatly from that in the Brahmaputra, as indicated by the presence of cyprinids such as *Tor tor tor* (HAMILTON, 1822), *Tor progenius* (MCCLELLAND, 1839), *Tor putitora* (HAMILTON, 1822) and *Neolissochilus* sp. The river bottom consists of fine sand and round stones of various sizes. This gravel bed heats up strongly during the day with the effect that daily water temperature can fluctuate within a 3.5°C range. In the rainy season the water level rises by several metres. After prolonged rainfall vast areas of the National Park can be flooded (PRASCHAG & FACHBACH 2001). The juvenile was in shallow water, in a cut-off side stream of the Jia-Bhoroli. The black soft-shell turtle lives here syntopically with *Pangshura sylhetensis* (JERDON, 1870)[1] and *Cyclemys oldhamii* GRAY, 1863.

According to testimonies of native fishermen, population densities are highest in the Brahmaputra itself. Especially river segments dispersed with islands are favoured. The muddy and turbid water of the Brahmaputra in Tezpur had a temperature of 22.7°C at 09^{45} h on 18 October 1999, and 23.8°C at 11^{00} h on 20 October 1999.

The tameness of black soft-shell turtles is species specific. Larger specimens, especially adults, are tamer than smaller animals (ANNANDALE & SHASTRI 1914, KHAN 1980, DAS 1991, 1995, RASHID & SWINGLAND 1997 and personal observations). *A. gangeticus*, as well as more shy juveniles of both species, keep themselves in the background in the pond at Nagsankar. Juveniles dive immediately upon disturbance. Old animals do not show any kind of aggression towards humans, and they also let themselves to be gripped. Several accounts have been published describing feeding at the temple tank in Chittagong (ANNANDALE & SHASTRI 1914, KHAN 1980, AHSAN et al. 1991, AHSAN et al. 1994, RASHID & SWINGLAND 1997). Soft-shell turtles inhabiting temple tanks in Assam are fed with bananas, white bread (Fig. 13), meat waste, rice-snacks, chips, and biscuits. Most frequently the food is thrown onto the water surface, more rarely it is handed over using wooden sticks. The animals are called by shouting "gol, gol, gol!", the word for banana in Assam, and they react to the movement of an up and down waving hand. The larger specimens even leave the water and climb up the stairs to reach the food. The animals are capable of swallowing their food on land. The juveniles, being more shy, eat the food which floats away from the banks. This can lead to aggressive interactions, ending most often in the escape of the smaller animal.

According to local fishermen, eggs are laid in the rainy season from July to October (ANNANDALE & SHASTRI 1914, PRITCHARD 1979, AHSAN et al. 1991, DAS 1991, 1995, RASHID & SWINGLAND 1997). *A. gangeticus* favours nesting on sand banks; the nests of *A. nigricans* and *A. hurum* are found predominantly in a mixed substrate of sand and clay. Data on reproduction are based on the Chittagong population (AHSAN et al. 1991, AHSAN & SAEED 1992).

Although the species is found in standing water, *A. nigricans* is to be considered as a representative of the large river turtle type (sensu MOLL & MOLL 2000). Such a categorisation is justified by its good swimming abilities and great size. Eggs are relatively small and numerous (AHSAN & SAEED 1992), and oviposition might occur several times a year, as in *A. gangeticus* (RAO 1986). The turtles leave water only rarely outside the nesting season. Warming up and basking occur at the water surface, or near the banks in shallow water, and only seldom on dry land in the immediate proximity of water.

According to our experience, *A. nigricans* has proven hardy in captivity. As for food, it will accept all kinds of fish and meat. Dried food in any form is taken only when the turtle is very hungry, and then rather selectively. Bananas, bread, popcorn, chips, biscuits, and equivalent unnatural food items which are taken eagerly at the temple ponds, are ignored. Already juveniles express a distinct intraspecific aggression, but show very friendly behaviour towards other species. Intraspecific threats with open jaw, and biting, are no rarity, especially when

[1] MOLL (1986, 1987) pointed out the significant differences between the small- and large-sized species groups of the genus *Kachuga*. We follow here DAS (2001) in recognising *Pangshura* as genus for the small species and *Kachuga* for the large species.

feeding. The opponent is fixed by the jaws, and the head is rapidly withdrawn. The claws are held next to the jaws, inserted into the wound and pushed hard forwards, away from the head. This can lead to deep wounds. The juveniles bite wildly in every direction when handled. The initial shyness of this species diminishes in no time, and it will soon beg for food. When hungry they try to climb out of the aquarium and as soon as they see the keeper, they stretch their head far out of the water. Contrary to *A. hurum*, but much like *A. gangeticus*, *A. nigricans* develops a certain curiosity, observes, but does not respond fearfully to activities in its immediate surroundings.

4. Discussion

The taxonomy of Asiatic soft-shell turtles is still insufficiently resolved. In an account and discussion about the giant soft-shell turtles of Hoan Kiem Lake of Hanoi (NIEKISCH et al. 1997), the authors conclude that giant soft shells belong to the rarities in zoological museums, which situation is even today reflected in the unclear systematic status of various populations because of the very small amount of reference material available for research. In the meantime the giant soft-shell turtle of Hoan Kiem Lake was described by HA DINH DUC (2000) as *Rafetus leloii* sp. n., one more Asian species known only from an artificial lake.
The lack of sufficient material and the resulting tentativeness of any taxonomic conclusions is especially relevant for the two widely ranging soft-shell turtle genera *Chitra* and *Pelochelys* attaining extremely large body proportions (NUTPHAND 1986, WEBB 1995), and also for the equally large-growing and apparently rare soft-shell turtle *Rafetus swinhoei* (GRAY, 1873). The latter species exemplifies how incomplete knowledge of ontogenetic stages can lead to taxonomic misconceptions, as this taxon was for a long time placed in synonymy of *Pelodiscus sinensis* (WIEGMANN, 1835) (e. g., POPE 1935, WERMUTH & MERTENS 1961, 1977). In this context attention should be drawn to the enigmatic forms already mentioned above, *Trionyx gangeticus mahanaddicus* and *T. sulcifrons*.

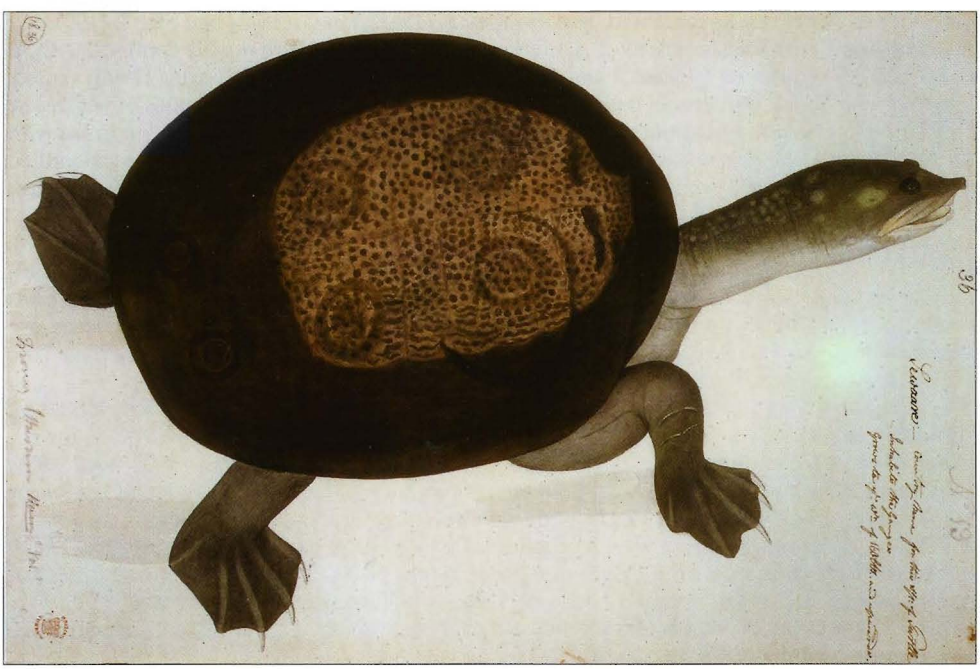

Fig. 16: *Trionyx sewaare*, Plate 36 water colour painting from HARDWICKE: "Reptiles of India, China, etc. Vol. I. Bequeathed by Maj. Gen. Hardwicke". Courtesy of Zoological Library of The Natural History Museum, London.

A further problematic taxon, currently regarded as a junior synonym of *Aspideretes hurum* (GRAY, 1830), is *Trionyx sewaare* GRAY, 1872 (Fig.16, see also Fig. 8). GRAY (1872) based the description of this species on an as yet unpublished plate (no. 36) by HARDWICKE. Although the six ocelli on the carapace and the pale flecks behind the eye point at *A. hurum*, according to the description of WEBB (1980: 67), the uniformly brown coloration of the carapace with a light-dark dotting in the region above the bony disc is less typical, as is, most importantly, the missing of the pale band at the base of the proboscis. The illustration, Fig. 4 of GRAY (1873: 50) features the skull of a juvenile with a wide lower jaw symphysis without a bony crest, which allows classification to *A. hurum* or a closely related species. Photographic evidence (Fig. 7, 8) from Assam shows that both *A. hurum* and "*T. sewaare*" occur syntopically with *A. nigricans*. This means that "*T. sewaare*" is either a good species or a mutant form within the overall variation of *A. hurum*, characterised by a pallid, poorly contrasting pattern, a weak or missing yellow band above the base of the proboscis, and a light-brown ground colour of the carapace, this matching the description by THEOBALD (1876).

4.1. Diagnostic characters

According to ANNANDALE (1912) and PRITCHARD (1979), the carapace and plastron of *Aspideretes nigricans* and *A. gangeticus* are indistinguishable. Generally, characters of the carapace and plastron are often not diagnostic for soft-shell turtle species (SIEBENROCK 1902, SMITH 1931). The differentiation of sternal callosities is highly variable (ANNANDALE 1912, GRAY 1872, SIEBENROCK 1902). If callosities of different taxa are compared, only equally sized or aged specimens should be used (GRAY 1872, SIEBENROCK 1902). An entoplastral callosity may be either present or absent both in *A. gangeticus* and in *A. nigricans*, and the character is not correlated with age or gender. Therefore, it can be well developed in smaller specimens whereas some individuals, considerably larger or older specimens, show no trace of it (ANNANDALE 1912).
A character which does not exhibit ontogenetic variation, and which is thus of use as a diagnostic character for species, is the lower jaw symphysis or the mandibular alveolar surfaces. Our personal observations verify results presented by ANNANDALE (1912), GRAY (1872) and SMITH (1931).
Hatchlings and juvenile specimens of *A. nigricans* (phases 1 and 2) are readily confused with *A. hurum*, larger individuals (phases 3 and 4) as easily with *A. gangeticus*. RASHID (1990) visited, together with MOLL, the temple tank in Chittagong, and mentioned two juveniles of which one could be unambiguously identified as *A. hurum*. BMNH 1994.449 is a juvenile *A. nigricans* with the locality data "Nazira, north of the Naga Hills, Eastern Assam, India", and was misidentified as *A. hurum*. DAS (1995) reported relatively large individuals of *A. hurum* in the Kamakshya Temple in Gauhati, where exclusively *A. nigricans* are kept, as mentioned previously.
BOULENGER (1889) regarded *A. nigricans* as a questionable synonym of *A. hurum* (Figs. 7, 8). KHAN (1987) supposed that the population in Chittagong is derived from *A. gangeticus* (Fig. 10) during long-time isolation. DAS (1997) is of the opinion that the taxonomic status of *A. nigricans* needs to be clarified, and infers that both juveniles and young adults of *A. nigricans* are superficially, inclusive of coloration, indistinguishable from *A. hurum*. This underlines the difficulties to diagnose *Aspideretes* species by external morphology until now.
The studies by MEYLAN (1987) have contributed considerably to our present knowledge of soft-shell turtles, and the taxonomic conclusions of his research, including implications for nomenclature, were uniformly accepted (ERNST & BARBOUR 1989, KING & BURKE 1989, IVERSON 1992, DAVID 1994). His work is based largely on osteological characters useful for resolving intrafamiliar phylogenies but not very practical for identifying species.
Especially concerning *Aspideretes*, the material available to MEYLAN was meagre, which questions the significance of the highlighted characters. Therefore, characters used in his paper for species and genus definition are selected and will be discussed as follows.
MEYLAN (1987, Tab. 3: 15) found only two out of 29 characters associated with the carapace which distinguish between the species of *Aspideretes*:
First, the number of neurals: *A. gangeticus* and *A. leithii* are supposed to have 8-9, *A. hurum* and *A. nigricans* are stated to feature 9 neurals.

Second, the neural reversal: From the 5th neural onwards a change in the typical shape is possible in that, the preceding (anterior) hexagonal neurals have the short lateral sides oriented caudally, whereas the short sides in the succeeding (posterior) neurals are oriented cranially. It is also possible that a quadrilateral neural is inserted at the "point of reversal". The neural reversal is supposed to occur always at the same position in *A. gangeticus* and *A. hurum*, and at different positions in other *Aspideretes* species. How this variability could be demonstrated for *A. nigricans* by inference from one carapace only (specimen BMNH 1929.12.23.1) is beyond comprehension.

A random check of five bony discs of *A. hurum* was undertaken to test to what degree these two characters are constant. The skeletal remains originate from a local turtle salesman in Bayder Bazar near Sonargaon, Bangladesh (NMW 31269: 1-5) which leads us to infer that they represent one population. Three animals featured 8 neurals (NMW 31269: 1, 3 and 5; Fig. 17 A, C, E), whereas two specimens had 9 neurals (NMW 31269: 2 and 4, Fig. 17 B, D). Accordingly, the number of neurals fluctuates between 8 and 9 also in *A. hurum*. The neural reversal point varies despite its supposedly occurring always at the same neural. NMW 31269: 2 and 4 show the reversal between 5th and 6th neural (Fig. 17 B, D), NMW 31269: 1, 3 and 5 between 6th and 7th neural (Fig. 17 A, C, E). The shell NMW 31269: 1, with a pentagonal 7th neural, and thus the 5th pair of pleurals enclosing the posterior side of the 5th neural, the quadrilateral 6th neural, and equally a short side of the 7th neural, is evidence that the reversal does not always have to run over a quadriform "diaphragm neural" but that the reversal can also occur via two pentagonal neurals, and that other irregularities may exist. The results indicate that, despite its possible phylogenetic importance, the neural configuration at least in *A. hurum* is so variable that it cannot be used in species determination.

Already SIEBENROCK (1902) wrote that the plastron of the Indian soft-shell turtle is hardly to be distinguished from *A. hurum* and *A. leithii*. The bony plastral elements are variable and

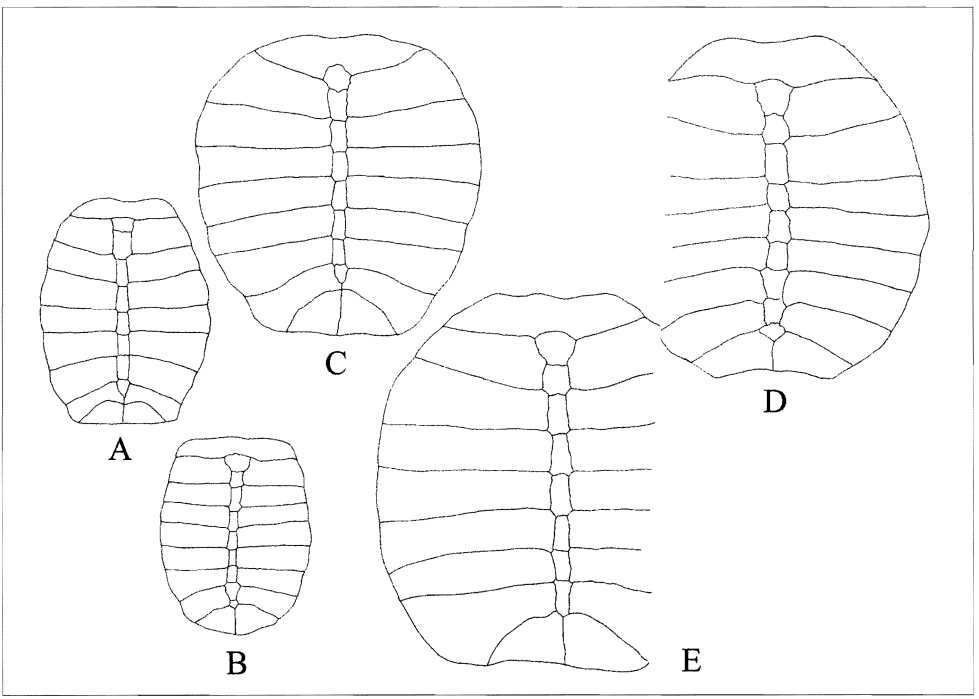

Fig. 17: Neural configuration of *Aspideretes hurum*. A = NMW 31269: 1; B = NMW 31269: 2; C = NMW 31269: 3; D = NMW 31269: 4; E = NMW 31269: 5. In relative size. The free, distal rib endings are not depicted. Illustration: R. GEMEL

go through ontogenetic changes (cf. plastra of *A. gangeticus* Fig. 1 and Fig. 3 in SIEBENROCK 1902): The distal shanks of the epiplastra of *A. nigricans*, positioned mutually apart from each other, are comparable to *A. gangeticus* and *A. hurum* of similar developmental stage. Whether the different distance between the epiplastra in juveniles, as compared to adults (Fig. 3), is ontogenetically determined, or whether it represents a part of the overall variation, should be clarified by examination of a larger series. The epiplastra may be in contact in the medial curved region in *A. nigricans*. The same condition may occur also in adults of *A. gangeticus* and *Nilssonia formosa*, and an epiplastral contact is especially pronounced in *Amyda cartilaginea*. However, in *Amyda cartilaginea* the distal epiplastral shanks are clearly longer than in the remaining Trionychini. In contrast to *A. nigricans*, in adults of other *Aspideretes* species these hooked bones are mostly narrow and slightly divergent or parallel, in some cases mutually inwards flexed and forming an S-shape at the anterior border. The entoplastral callosity in *A. nigricans* is, if present at all, small.

A sexual dimorphism in shell shape is also seen in adult *A. gangeticus*, but the difference between sexes is not as pronounced as in *A. nigricans*. *Dogania subplana* (GEOFFROY SAINT-HILAIRE, 1809) exhibits a similarly parallel-edged shell like males of *A. nigricans*. Despite the similarity, this species has however an especially widened posterior cartilaginous part which contributes to a different shell shape. *D. subplana* also remains considerably smaller, and is well separated from *Aspideretes* by a series of further characters.

Skull

At phase 4 black soft-shell turtles can develop broad jugal arches for the strongly hypertrophied jaw adductors, apparently related to grinding hard-shelled food. Fig. 4.4. shows an adult specimen in Chittagong, whose jaw adductors are so massively developed that the parietal and supraoccipital regions of the skull appear as a groove in the middle. According to observations until now, most adult individuals feature wide skulls with grinding jaws. Only once was an animal with a narrow head documented (Fig. 18).

The skull depicted in AHSAN et al. (1994) shows widely spread zygomatic arches and is supposedly referable to a very old animal. Fig. 4.4. and Fig. 5.4. show at the same time the relatively anterior location of the eyes as well as the very short proboscis, reminiscent of the genus *Pelochelys*.

After BOULENGER (1889) demonstrated the sharp-edged jaw structure (fish-feeding) and the broad triturating surface (mollusc-feeding) at least for the species *Trionyx triunguis*, *Amyda cartilaginea* and *Pelodiscus sinensis*, DALRYMPLE (1977) studied the intraspecific variation of feeding mechanisms in *Apalone ferox* (SCHNEIDER, 1783) and its effect on skull structure. Accordingly, the different jaw formations in one species can be understood as physiological adaptations of the skull to feeding mechanisms, which become more divergent with age and growth. *Apalone ferox* and *A. spinifera* (LESUEUR, 1827), among the New World species, exhibit skull dimorphism which is detected even in smaller skulls of males and young females. ANNANDALE (1912) did not note the skull dimorphism in *Aspideretes* specimens from the Ganges region, and points to a sturdy, robust skull as being typical for *A. gangeticus*, and a more slen-

Fig. 18: Slender-headed adult *Aspideretes nigricans* male on opposite river bank in Kaziranga National Park. Photo: P. PRASCHAG

der skull as typical for *A. hurum*. He also remarks that the width of the lower jaw symphysis of soft shells from the Ganges area is constant in relative terms, and independent of age and skull dimorphism and that thus it is a good diagnostic character. The width of the lower jaw symphysis (Fig. 19) relative to diameter of the eye can be used for species determination in the genus *Aspideretes* up to a certain degree:

Fig. 19: Comparison of lower jaw symphyses, from upper left corner to lower right corner: *Aspideretes hurum* (BMNH 86.8.26.2), *Aspideretes gangeticus* (BMNH 86.8.26.1), *Trionyx phayrei* = *Amyda cartilaginea* (BMNH 68.5.18.2), and *Aspideretes nigricans* (BMNH 1929.12.23.2). Photo: P. PRASCHAG

The width of the symphysis in *A. hurum* (Fig. 19) is always broader than the diameter of the eye, because of the typical "beak-like" elongation of the lower jaw. The alveolar surfaces are often yellowish, whitish in *A. gangeticus*. Additionally *A. gangeticus* has a blunt, uniformly rounded lower jaw, and the symphysis (Fig. 19) is narrower than the eye diameter. On the contrary, the elevated inner edges of the mandible could not be found in any specimen of *A. gangeticus* in the NMW collection (n = 13), indicating that this feature is not a reliable character. In *A. nigricans* the symphysis is approximately as wide as the diameter of the eye, and in *A. leithii* slightly wider. Both species take an intermediate position between *A. hurum* and *A. gangeticus* regarding this character.

In addition to its width, the special structure of the symphysis contributes useful characters. All *A. nigricans* examined by us possess a bony, sagittally oriented edge (Fig. 1, Fig. 19) in the trough-shaped depression of the lower jaw symphysis. The thin bone-ridge on the symphysis of the lower jaw bone is equally distinct as on the alveolar surfaces covering it. Because of this, the character can be used for species determination also with live animals. A comparison with other Asian trionychids shows that there is an as distinctly formed ridge in most *Amyda cartilaginea*, too. NMW 1874 from Buitenzorg, Java, which can be classified into this species without question according to its epiplastral configuration, is an exception, supporting the view that *Amyda cartilaginea* is a polymorphic species. The named specimen may be the reason of SIEBENROCK's (1913) remark, that this character is not significant in *Amyda*.

Examination of the mandibular symphysis in related species revealed that this bone-crest is not, or very weakly, expressed in the remaining species of *Aspideretes*. The material from BMNH correlates with respect to this character with the 13 *A. gangeticus* at various developmental stages from NMW. Also, two juvenile *A. hurum* from Pakistan NMW30235: 4, 5, and *A. leithii* NMW 30202 (juv.), as well as NMW 30234, do not show the ridge on the mandibular symphysis. It is weakly visible in *Nilssonia formosa* (NMW 30235: 1), and better still in living animals. BOULENGER (1889) and SMITH (1931) detected in *A. gangeticus* a short perpendicular protuberance originating from the strongly elevated inner edges of the mandible, and running towards the symphysis, and they expressly pointed to the absence of this bone-ridge in *A. leithii* and *A. hurum*. In addition, SMITH (1931) emphasised the strong expression of this character in *A. nigricans*. These inferences agree with our observations, and they are in congruence with results of ANNANDALE (1912), who stated that he had examined several hundred living animals, and a large series of skulls. In his key (pp. 156, 157), ANNANDALE distinguished between *A. nigricans* with a bone-ridge, and others without it or in which it is only very weakly expressed.

The more astonishing is the grading of this character by MEYLAN (1987), who codes it as "strong and present" for *A. gangeticus*, *A. leithii*, and *A. hurum*. He cites this feature also as

being a useful character to infer phylogenetic hypotheses among trionychids (MEYLAN 1987: p. 45, Tab. 17), and uses it to define the genus *Aspideretes* (MEYLAN 1987: 92), without discussion of ANDERSON's (1912) contradicting account, despite citing it.

Pattern, coloration, soft structures

Structures of soft parts and colour characteristics are especially important discriminating characters of trionychid species that are hard to separate from one another using morphological means (DAS 1985, 1991, 1995). Thus FARKAS (1992) was able to detect a *Rafetus swinhoei* in a series of *Pelodiscus sinensis*, based mainly on colour criteria. Soft parts, for example the warts in the neck region in *A. leithii*, *Palea steindachneri* (SIEBENROCK, 1906), or *Apalone spinifera*, can be taken as species specific.

The change in colour is the product of interactions between the dermal guanophores, xanthophores, and melanophores. Light-dark changes are primarily induced by an aggregation or dispersion of melanin inside the melanophores (BARTLEY 1971). The development of coloration in *A. nigricans* is traced to a species specific dispersion of melanin. Excluding the well-known occurrence of melanism at old age, deviations from the typical condition exist among Asian softshell turtles: We detected melanism in individual adult, but not extremely old animals, among *A. hurum* and *Lissemys punctata andersoni* on markets in Dhaka and Khulna, Bangladesh.

THOMAS (1967) showed a reverse colour change in *Lissemys punctata andersoni*. Similar physiological colour changes such as adaptation to light intensity, reflected light, lighter or darker bottom, or temperature can be observed under aquarium conditions in soft-shell turtles of the genus *Aspideretes*, too. This colour change does not affect the pattern, however. Discernible, season dependent, morphological colour change as seen in males of *Callagur borneoensis* (SCHLEGEL & MÜLLER, 1844)(MOLL et al. 1981) is not known for soft-shell turtles, but colour differences associated with gender do occur in *Apalone mutica* (LE SUEUR, 1827) and *Apalone spinifera* (WEBB 1962). SACHSSE (1971) noted a remarkable change in pattern among juvenile *Chitra indica*.

Pigments of the ocelli, covering the leathery skin over the bony disc, can be well distinguished on the bone of especially young animals, like in the semiadult *A. hurum* (NMW 31269: 1 and NMW 31269: 2). We know this phenomenon also from both *Morenia* species which show clear pigmentation of the bone when scutes are removed.

4.2. Phylogenetic relationships

To understand phylogenetic relationships, one has to take into account also observations based on living animals, their ecology, and behaviour. Osteological studies yield a surprisingly close phylogenetic relationship of *Amyda cartilaginea* with *Chitra* and *Pelochelys*, for this reason these taxa are classified into a common tribe Chitrini by MEYLAN (1987) and GAFFNEY & MEYLAN (1988). *Amyda cartilaginea* is in any case a variable and adaptable species which can also develop wide-skulled forms with grinding jaws. It occupies many different aquatic biotopes (LIM & DAS 1999), and the species can be regarded as an unspecialised representative, a generalist among trionychids. There are several allusions to suggest that we are dealing with a polymorphic species (i. e. AULIYA 2000). In contrast, *Pelochelys* and *Chitra* are characterised by an extremely flat shell with a comparably wide cartilaginous rim. Their probosci are short and the eyes shifted strongly towards the anterior. The long skull, with an extreme posterior position of the jaw articulation and the specially structured hyoid, enables a specialised suction snapping. The first dorsal vertebra, located anteriorly due to the narrow nuchal bone, has the effect that the neck can be stretched out very far. This construction indicates these two species as efficient fish hunters. SACHSSE (1971) has accounted for the unusual behaviour of juvenile *Chitra*. *Pelochelys* is not only distributed along the delta regions of large rivers, but also tolerates living in the sea. Together with a number of additional characters, representatives of these two genera are to be understood as a specialised side-branch within trionychids.

Nilssonia, equally an Asiatic "ocellated soft-shell turtle", is hard to distinguish from *Aspideretes* and *Amyda*, but is nevertheless placed as a close relative of *Aspideretes* by MEYLAN (1987), and

can be seen as more progressive than *Aspideretes*, based on the fused first neurals, the relatively narrow nuchal bone, and consequently, the far anteriorly positioned first thoracic vertebra.
The small-sized Malayan soft-shell turtle *Dogania subplana*, too, shows an ocellated pattern, but is taxonomically well delimited by a series of characters. Therefore, a series of non-osteological findings support the view that the four *Aspideretes* species, together with *Nilssonia formosa* and *Amyda cartilaginea*, form a group of taxa which are hard to distinguish from one another. These six species constitute a soft-shell turtle group of relatively unspecialised generalist feeders with a similar appearance, with an ocellated pattern which develops into a reticulate pattern or fades away with the progress of age induced melanism.
Karyological evidence available until now (BICKHAM et al. 1983) is insufficient for resolving phylogenies from this perspective. We look forward to seeing phylogenies within Trionychini, and especially within the genus *Aspideretes*, based on molecular techniques.

4.3. Vulnerability and conservation

Assuming that the population in Chittagong is the only one in existence, AHSAN (1997) demands that animals hatched at the temple tank should be reared to be used as basis for new populations, and to save the species from extinction.
In Bangladesh, where the Chittagong tank population is watched by the mosque's administrative personnel, the species is additionally included in Schedule III of the Bangladesh Wildlife Preservation Act of 1974 (DAS 1991). Internationally, it enjoys the strongest protection in Appendix I of CITES, and in Annex A of the ordinance no. 2307/97 of the European Union. *Aspideretes nigricans* is listed in the action plan of the IUCN (1991) in the category of species with a small living area, and it is thus included in a species conservation project. BURKE et al. (2000) consider *A. nigricans* together with *Pseudemydura umbrina* SIEBENROCK, 1901 of Western Australia as being the rarest turtles in the world.
The main aims must be directed at wild populations. Although the catching of turtles is principally prohibited in Assam, especially trade in soft-shell turtles remains extensive (Fig. 20). *Chitra indica*, *Pelochelys cantorii*, *A. hurum*, and *A. nigricans* are given priority as a source of protein and reach the highest prices. Because of a strong fish taste, meat from *Aspideretes gangeticus* is less beloved, and consequently cheaper. CHAUDURI (1912) states the opposite, but all fishermen asked by us confirm the lower price of *A. gangeticus*. The large soft-shell turtles are caught with baited and unbaited lines equipped with dozens of hooks. Smaller animals often end up as by-products in fishnets. Additionally, eggs are collected on the sand banks and islands in co-ordinated fashion.
The cheap land on the riverine islands is often occupied by refugees from Bangladesh who lead here a battle for survival, which includes collecting turtles and their eggs whenever opportunity arises, though Moslems are in principle not allowed to consume meat derived from amphibious living creatures. NUGENT (1993) tells about turtle catchers in the Brahmaputra, who hunt using boats. They follow the air bubbles of diving turtles and catch them with a net and trident. If

Fig. 20: Wild-caught *Aspideretes nigricans* at the northern bank of the Brahmaputra. Anterior and posterior extremities are tied together. Photo: P. PRASCHAG

the turtles are wounded or surface for air, a loop is pulled around their neck. Whole village communities are said to obtain their livelihood from hunting turtles.
All fishermen complain about the threatening decline of populations. To satisfy the demand in turtles, fishermen are bound to travel longer and longer distances, far away from the wholesale centres and risk penetration into protected areas.
The large Southeast Asian soft-shell turtles are not threatened only by over-fishing. The industrial quarrying of nesting banks with large machinery poses a serious threat. MOLL & MOLL (2000) noted such changes at almost all larger streams in Bangladesh, India, Indonesia, Malaysia, and Thailand. In Bangladesh along the Kali Ganga and the Padma River in Dhaka province *A. hurum* is affected by such activities. In contrast, riverine turtles under the influence of the protected temple districts can directly profit from this protection, and they are remarkably more common in these regions (MOLL 1985, MOLL & MOLL 2000). According to our observations, *Aspideretes nigricans* shows still relatively good population densities in parts of the Brahmaputra. To promote long-term survival, clarifying studies and targeted conservation projects are essential. MOLL (1985), among others, has presented suggestions and accordant recommendations for *Pelochelys cantorii* and other riverine soft-shell turtles in Southeast Asia. These could be adopted in essence for turtle populations in the Brahmaputra as well.

5. Perspectives

The discovery of *Aspideretes gangeticus* in Afghanistan by SCHNEIDER & DJALAL (1970) exemplifies how deficient our knowledge of the distribution of Asian soft-sell turtles is. *A. gangeticus* is the best known species of the genus. It was at least until recently relatively common in the Indus region, and intensively eaten from historic times until today (MINTON 1966, MERTENS 1969). Our finding that the allegedly highly endangered species *A. nigricans*, thought to be endemic to a single locality, the Mosque water tank in Chittagong, Bangladesh, is a wide-ranging, common species in the wild in Assam, India, underlines this situation.
Ecological studies would be needed to portray water system structures, to study habitat preferences in a constantly changing environment, and to compare nutrition in different regions along the species' distribution. Research on reproduction in wild populations is of great importance, especially with respect to the effects from strong hunting pressure for commercial purposes by fishermen and consequent over-exploitation. *A. nigricans* could potentially end up undetected in the international trade, together with the equally CITES I listed *A. gangeticus* and *A. hurum*. In a recent list compiled by Pro Wildlife (ALTHERR & FREYER 2000) *A. leithii* appears among species which are used in traditional Chinese medicine. The distribution cited in this list for *A. leithii*, "India and Pakistan", suggests that other species of *Aspideretes* are lumped under one heading in the international trade.

6. Key to species in the genera *Aspideretes*, *Amyda*, and *Nilssonia*

Currently many diagnostic characters for soft-shell turtles are based on osteological characters (e. g., MEYLAN 1987). This is not helpful in identifying live or entire alcoholic specimens and contributed much to nomenclatural and taxonomic confusion. To improve this situation, we present in the following a key for the species of the genera *Aspideretes*, *Amyda* and *Nilssonia* based on external morphology.

1 Top of head with craniad oriented lines and stripes, without reticulated pattern; carapacial ocelli without yellow ring: 2
1' Top of head without stripes; carapacial ocelli of juveniles with yellow ring featuring dark to black borders: 3
2 Lower jaw symphysis shallow; wart-like tubercles at anterior rim of carapace; dark stripe running from eye caudad, and two or three pairs of dark lateral head stripes (in adults often not visible anymore); carapacial ocelli mostly small; juveniles with yellowish carapace: *Aspideretes leithii*

2' Lower jaw symphysis especially small, smaller than diameter of eye; inner side of symphysis can stand out as edged; top of head olive-green coloured; several diagonal black stripes oriented anteriorly towards the top of the head may fuse to form a rhomboidal pattern; carapace grey-green (Indus region) or olive-green (Ganges region) with dark reticulated or vermiculated pattern: *Aspideretes gangeticus* (Fig. 10)

3 Lower jaw symphysis with bony crest; from approximately 20 cm carapace length onwards only indistinct or invisible ocelli: 4

3' Lower jaw developed into "beak-like" wide symphysis without bony crest, considerably longer than diameter of eye; also adults feature ocelli (except for very old or melanistic individuals); base of proboscis with yellow or grey band; distinct yellow postorbital flecks; proboscis oriented downwards: *Aspideretes hurum* (Figs. 7, 8)

4 Ocelli absent at all ages; bony ridge on lower jaw symphysis shallow, sometimes only its trace is present, occasionally absent; carapace mostly speckled with yellow; head with yellow, never dark-bordered, dots and/or flecks: *Amyda cartilaginea* (Fig. 6)

4' Ocelli present at least to a carapace length of 20 cm: 5

5 Bony crest on lower jaw symphysis shallow; small postorbital and narrow temporal flecks present, the last of which is extensive and reaches median line of top of head, only in small juveniles; from about 10 cm carapace length onwards black flecks on head distinguishable from grey ground colour; never yellow speckles on carapace: *Nilssonia formosa* (Fig. 9)

5' Bony crest on lower jaw symphysis distinctly developed, visible in an open mouth (Fig. 1); postorbital and temporal flecks present in small juveniles and may persist until approximately 45 cm carapace length; in specimens over 45 cm carapace length, sometimes already in smaller ones, white temporal fleck expanding with age; in specimens from 15-45 cm shell length, yellow speckles on carapace: *Aspideretes nigricans*

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