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Evidences of cheloniophagy by early hominid (*Homo erectus*) during middle of pleistocene from beds of trinil's layers in central Java (Indonesia), with an updated list of trinil's testudines, and a redescription of *Duboisemys isoclina* (Dubois, 1908)

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Abstract

This paper based on a case study, which was accomplished at the beds of Trinil's layers in central Java (Indonesia). The collections of fossils from this site support the evidences of turtle's consumption by hominin (*Homo erectus)* of the middle Pleistocene epoch. The taxonomy and identification of Chelonian fauna accompanying of the *Homo erectus* of Trinil's layers in central Java were taken and described from this site. The illustration and revise systematic and taxonomic status of fossil records of *Duboisemys isoclina* (Testudines: Geoemydidae) of the middle Pleistocene deposits from this site were described and completely illustrated during this study. The manufacturing of stone tools and their use to access animal tissues by hominins of middle Pleistocene marks the origin of a key adaptation in hominin evolutionary history. We found situ archaeological assemblage from the beds of Trinil's layers in central Java (Indonesia), which provides a unique combination of faunal remains, some with direct evidences of butchery while some with indirect. This site provides the oldest in situ evidences that hominid (*Homo erectus)* predated and enjoyed access to carcasses of terrestrial and aquatic testudines' that they butchered. The fossils of following Chelonian's species were discovered from the beds of Trinil layers in central Java: *Chitra chitra javanensis*, *Pelochelys cantorii*, *Amyda cartilaginea*, *Batagur affinis affinis*, *Orlitia borneensis*, *Duboisemys isoclina* and *Megalochelys* sp.

Keywords: Cheloniophagy, *Homo erectus*, Beds of Trinil's layers, Middle Pleistocene, Redescription of *Duboisemys isoclina* (Dubois, 1908)

1. Introduction

The descent of the genus *Homo* from Australopithecus took place in East Africa over 3 million years ago. Of the earliest members of the genus *Homo*, the best-known species are *Homo habilis*, *Homo rudolfensis*, and *Homo erectus*. The characters and distribution of *Homo habilis* and *Homo rudolfensis* into *Homo erectus* are influent (Spoor et al., 2007; Villmoare et al. 2015)[1-2]. The first two species are the most primitive compared to what is known about *H. erectus*, little is known about how they differ in anatomy and behavior from one another and from preceding australopiths. *H. erectus* signifies a major shift in hominin evolution, most notably through increased brain and body size and increasingly complex tools and behaviors. Already the cheloniophagy by *Homo rudolfensis* had been evidenced (Karl, 2012)[3]. During the Early Pleistocene, 1,900,000 ybp, the hominins *Homo ergaster* and *Homo erectus* appeared in Africa. Some 1,800,000 ybp *Homo erectus* migrated out and spread widely through the Middle East, the Caucasus, Southern Europe, Southern and Eastern Asia (Mainland China, Possibly differentiating as *Homo pekinensis*), and the Indo-Australian Archipelago as far as Flores (Possibly differentiating as *Homo floresiensis*), Survived on Java until ca. 70,000 ybp (Possibly differentiating as *Homo soloensis*); did not reach Japan and Australia. The presence of a giant tortoise on Java between 2,000,000 and 1,200,000 ybp was considered to be indirect evidence that *Homo erectus* had not yet reached the island at that time (Van den-Bergh, 1999)[4], Since giant tortoises were easy prey for hunter-gatherers and rapidly became extinct on islands where hominins settled, as noted by (Sondaar, 1987)[5]. *Homo erectus* apparently arrived in Java ca. 1,500,000 ybp (Joordens et al., 2009)[6], and very possibly caused the extinction of various species. Findings of *Homo erectus*, originally called *Pithecanthropus erectus* later *Anthropithecus erectus* were reported from South Africa, Indonesia and many other parts of the old world. The locations extend from Africa to Asia and Europe. (Joordens et al., 2009)[6] used the *Homo erectus* site of Trinil as a case study to investigate how research questions on possible dietary relevance of aquatic environments can be addressed. Faunal and geochemical analysis of aquatic fossils from Trinil "Hauptknochenschicht" (HK) fauna demonstrates that Trinil at ~1.5 Ma contained near-coastal rivers, lakes, swamp forests, lagoons, and marshes with minor marine influence, laterally grading into grasslands (Joordens et al., 2009)[6]. The sediments of the Trinil basin were deducted from the Solo River, which runs since the Middle Pleistocene in the same basin. Based on the findings of rhinoceros of Trinil, it can be deduced as an open to forested landscapes area, but also macaques and leaf monkeys were found. The turtles are invariably river inhabitants. More turtle material of other Javanese sites such as Sangiran, Kedung Brubus or Kendeng hills north of Mojokerto is known (Hooijer, 1946; Karl, 1983 and Soergel, 1913)[7-9]. From the analysis of sediment residues at the skull of the Modjokerto Kid in 1936, a dating attempt was done years later for Sangiran and yielded an age of 800.000 years and for Trinil 2 an age of 400.000 years ago. Older dated findings up to an age of about 1.7 million years ago were controversial discussed at the time positioning. They are now of 1,000,000 to 500,000 ybp dated by (Aimi and Aziz 1985)[10] or 1,500,000 to 900,000 ybp according Joordens et al., (2009)[6]. The dating of *Homo erectus* reaches into the middle Pleistocene. This period is therefore especially significant, because humans already developed a stone tool industry here. They succeeded in domination and control of fire and the food spectrum was extended by regular carnal food, which in turn required effective hunting techniques. Therefore, all remnants of the accompanying fauna of hominids are also from the archaeo-zoological point of view interesting. Because of the high fractioning degree of the mostly very thick tortoise shells these remains from the Trinil-layers are food remains of *Homo erectus* (Jaekel, 1911)[11]. Wild chimpanzees (*Pan troglodytes troglodytes*) exploit tortoises (*Kinixys erosa*) via percussive technology which provide systematic descriptions of the first observations of chimpanzee predation on tortoises with a distinct smashing technique, and resulted frequently in food sharing with other group members (Pica et al., 2019)[12]. Quite early the turtle populations had been influenced by the consumption of early hominins and the cheloniophagy is already proved with early hominids and is extended by the described material by (Blasco, 2008 and Karl, 2012) [3 & 13]. The present study is an attempt of a continuation for possible clues and evidences of cheloniophagy by early hominin (*Home erectus*) in Trinil area of Java.

2. Materials and methods

Morphological data have traditionally played a very key role in inferring species phylogeny but this has been replaced recently by molecular data due to multiple of factors, perhaps most prominently due to the efficiency and low cost of sequence data acquisition and the development of analytical methods to deal with more characters and finding phylogenetic relationship with other species. This is unfortunately leading to a large asymmetry in the studies using either type of data, while morphological data can still provide an important framework to assess molecular trees (Giribet, 2015) [14]. Molecular data testing is impossible for fossil materials, for this reason we followed the methods of Hervet (2004a-b)[15-16] for current study which based on well-defined morphological characters. For referred specimens see appendices (Appendix 1-3). We followed the methodology of (Blasco, 2008) [13] for the anthropogenic damages and other clues of cheloniophagy by *Homo erectus* from fossils of turtles of the study area.

Terminology

The terminology on the carapace and plastron of an Emydid turtle corresponds to the following abbreviations (Fig. 1):

Carapace plates (bones): Nuchal = nu, neurals = n I - n VIII, pleurals = pl I - VIII, peripherals = pe I - pe XI, metaneurals = mn I - II, pygal = pyg.

Carapace scutes (horny shields): Cervical = ce, centrals = c 1 - c 5, laterals = l 1 bis l4, caudals = ca.

Plastral plates (bones): Epiplastrals = epi, entoplastron = ento, hyoplastron = hyo, hypoplastron = hypo, xiphiplastra = xiphi.

Plastral scutes (horny shields): Gulars = gu, humerals = hu, pectorals = pec, abdominals = ab, femorals = fe, anals = an, red = inguinal scutes.

Abbreviations: CL — carapace length, LWI — length to width index, LHI — length-height-index, BI — bridge index, l — length, b — width, bant — anterior width, bpost — posterior width, lant sin, — left anterior length, lant dex — right anterior length, lpost sin — left posterior length, lpost dex — right posterior length, lmed — median length, bmax — maximum width.

Institutions

SRQW = Senckenberg Research Institute, Frankfurt am Main, Dept. Quaternary Paleontology, Weimar/ formerly IQPW = Institute of Quaternary Paleontology Weimar; MB = Natural History Museum, Berlin/ Leibniz Institute for Evolution and Biodiversity Science; RMNH.RENA = Rijksmuseum van Natuurlijke history/ Netherlands Centre for Biodiversity “Naturalis", Leiden, Dubois collection.

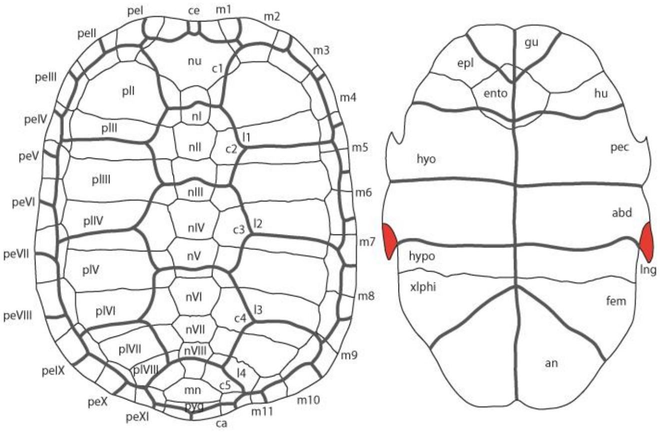

Fig 1: Terminology of the carapace and plastron of an emydid turtle, *Emys orbicularis* (explanations in the text).

3. Results

3.1 Sub-fossil and recent turtles of java

The current updated list of Chelonian fauna of Java:

Geoemydids (Hard shell turtles)

Cuora amboinensis couro (Schweigger, 1812), *Cyclemys dentata* (Gray, 1831), *Cyclemys shanensis shanensis* (Annandale, 1918), *Malayemys subtrijuga* (Schlegel and Müller 1845), *Notochelys platynota* (Gray, 1834) *and Siebenrockiella crassicollis* (Gray, 1831).

Trionychids (Soft-shell turtles)

Amyda cartilaginea (Boddaert, 1770), *Chitra chitra javanensis* (McCord & Pritchard 2003)[17], *Dogania subplana* (Geoffroy and Saint-Hillaire, 1809) *and Pelochelys cantorri* (Gray, 1864), being fewer than that of Sumatra and Borneo.

The sub-fossil Chelonian fossils from Pleistocene epoch of Java (Table 1)

On the other hand, previous paleontological researches on the Pleistocene of Java have revealed presence of several extinct taxa (Karl, 1983; Karl and Staesche, 2006; and TEWG, 2015)[8 & 18-19]. The following updated and valid taxa list of testudines' which were present during the Pleistocene in Java according to TEWG (2015)[19]:

Trionychidae

- *Chitra chitra javanensis* (McCord and Pritchard 2002) *[syn. Chitra selenkae* (Jaekel, 1911) (nomen suppressum)] Comment: Synonymized with *Chitra indica* by Karl (1987) and with *Chitra chitra* by McCord and Pritchard (2003), who noted that *C. selenkae* was essentially a nomen oblitum; the name was later suppressed by the ICZN (2005).
- *Pelochelys cantorii* (Gray, 1864) [syn. *Chitra minor* Jaekel 1911] Comment: Synonymized with *Chitra indica* by Karl (1987) and with *Pelochelys cantorii* by McCord and Pritchard (2003).
- *Amyda cartilaginea* (Boddaert, 1770) [syn. *Trionyx trinilensis* Jaekel 1911] Comment: Synonymized with *Trionyx cartilagineus (= Amyda cartilaginea)* by Karl (1987); agreed by van Dijk (unpubl. data).

Geoemydidae

- *Batagur affinis affinis* (Cantor 1847) [syn. *Batagur siebenrocki* (Jaekel, 1911)] Comment: Synonymized with *Batagur baska* by Karl (1987) prior to the taxonomic split between *B. baska* and *B. affinis*. Synonymization updated to reflect current taxonomy and distribution of *Batagur*.
- *Duboisemys isoclina* (Dubois, 1908) [*Hardella isoclina* Dubois, 1908, *Mauremys isoclina* (Dubois, 1908)] Comment: Redescribed and reassessed as *Clemmys* by (Williams, 1957), treated as *Mauremys* by (Das, 1997; Hoogmoed et al., 2010). However, its generic allocation needs further reassessment owing to the presence of several morphological differences from *Mauremys* (Karl, Philippen and Takahashi, unpubl. data). The species is a component of the Trinil HK Fauna (Joordens et al., 2009), considered to be 1,500,000 to 900,000 ybp in age.
- *Orlitia borneensis* (Gray, 1873) [syn. *Batagur signatus* Jaekel, 1911] Comment: Synonymized by (Karl, 1987).

Testudinidae

- *Megalochelys sp. [Colossochelys atlas* (Falconer and Cautley, 1844), *Megalochelys cf. sivalensis* (Falconer and Cautley, 1837)] Comment: Considered by Sondaar (1981, 1987) and Setiyabudi (2009)[50] to probably be a distinct species (Plate 1). See also Vlachos (2019)[48] and Naksria et al. (2019)[49].

Plate 1: Photographs of one of the complete fossil's femur of *Megalochelys* sp./ NCBN — Dub 11705: Left femur from Kali Glagah, Tegal, Western Java, 18.11.1932, ex coll. von Koenigswald to Prof. Brongersma.

Table 1: The distribution and finding localities of all turtle species from middle of Pleistocene at Java (Indonesia)

Area	Locality	*Batagur*	*Duboisemys*	*Orlitia*	*Chitra*	*Pelochelys*	*Amyda*	*Megalochelys*
Kendeng Mountains	Kedung Brubus	✓						
	Kedung Bumbu					✓		
	Pandean					✓		
Middle Java	Kedoeng Panas		✓					
	Trinil	✓		✓	✓	✓	✓	
	Sambungmacan	✓						
	Bogmi Aloi	✓						
	Bumiayu							✓

These findings indicate that Java had much richer testudine's fauna than the present. Thus, detailed morphological, systematic, and taxonomic studies on these fossils will contribute to appropriate understanding of past turtle species richness. In addition, results of such studies will offer valuable data for reinforcement or verification of the Quaternary paleo-geographical hypotheses of the Indonesian archipelago as well as implications for aquatic environment for the Pleistocene hominid. Ingicco et al., (2018)[20] describes the results of recent excavations at Kalinga (Cagayan Valley, N-Luzon), e.g. 57 stone tools and an almost-complete disarticulated skeleton of *Rhinoceros philippinensis* with clear signs of butchery, together with other fossil fauna remains attributed to stegodon, Philippine brown deer, monitor lizard and also fresh-water turtle. All these finds originate from a clay-rich bone-bed, dated to between 777 and 631 ka (electron-spin resonance methods, applied to tooth enamel and fluvial quartz). This evidence pushes back the proven period of colonization of the Philippines by 100s of 1000s of years; it suggests that early overseas dispersal in Island SE- Asia by premodern hominins took place several times during the Early and Mid-Pleistocene. Continuing information to the faunal structure and their actual interpretations presented by Geer et al., (2018)[21]. According the authors Xenocyon was the only canid of early and Middle Pleistocene of Java and evolved considerable dwarfism, due to filtered insular conditions of Java. The direct environment of *Homo erectus* of Trinil HK has an insular signal and the degree of endemism of terrestrial mammals of the earliest Middle Pleistocene horizon of the site Trinil HK, which has also yielded *Homo erectus* fossils, indicates that during this period, Java was marginally isolated which allowed for a corridor dispersal to the island. The nature and degree of isolation may have been similar to that of Late Pleistocene Sicily, but of a longer duration, given the higher degree of dwarfism of the stegodon, antelope and canids. The following continentalization enabled the invasion by mainland terrestrial mammals, as is seen in younger layers at Trinil, and eventually by *Homo sapiens* and *Cuon* in the Late Pleistocene. The evidence of *Duboisemys* as an endemic freshwater turtle species supports the hypothesis of a longer island history of Java. In fact, they are trying to clarify its appropriate taxonomic and phylogenetic position within the family Geoemydidae.

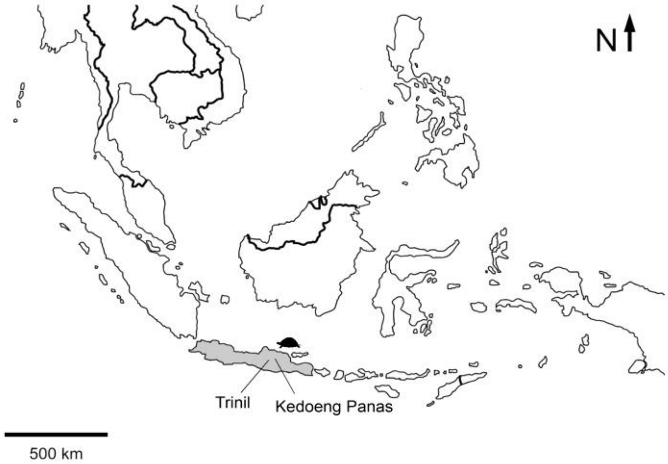

Fig 2: Geographical position of the type locality of *Duboisemys* n. gen. [D. isoclina (Dubois, 1908)]: Kedoeng Panas at Java in Indonesia (Courtesy by; Meijer, 2014).

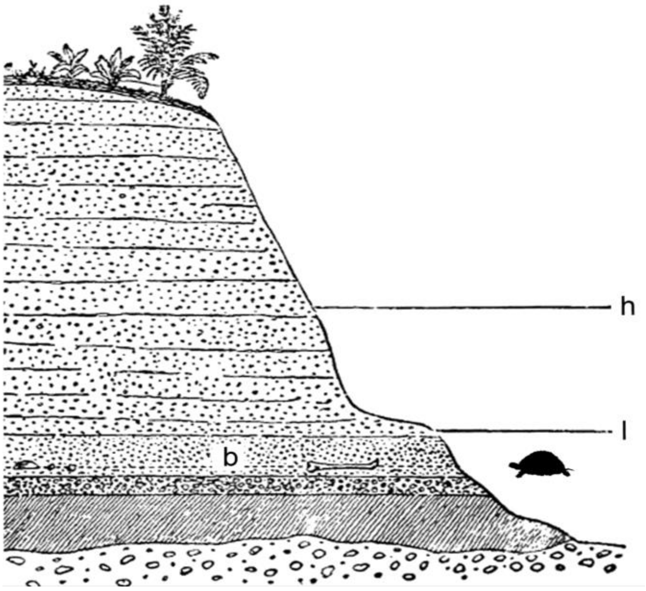

Fig 3: Trinil Beds/Trinil layer, 1,500,000 to 900,000 ybp, type horizon of *Duboisemys* n. gen. [*D. isoclina* (Dubois, 1908)]. Map adapted from Dubois (1908). h — high water line of the Solo river, l — low water line of the Solo river, b — Trinil HK Fauna (Hauptknochenschicht fauna).

3.2 Patterns of Turtle Consumption and Butchery Process

Blasco (2008) [13] described evidences of the acquisition and use of tortoises (*Testudo hermanni*) for food in the form of: (1) cut marks on limb bones and ventral surface of the carapace and plastron; (2) presence of burning traces on tortoise skeleton and shell; (3) elements of anthropogenic damages on carapace and plastron: crash pits and notches as well as impact flakes; and (4) human tooth marks on limb bones. This paper tries to examine the possible patterns in the tortoise consumption sequence from Level IV of Bolomor Cave in Spain and improves data on the butchery process and tortoise consumption in the Late Middle Pleistocene in Europe. The condition of our turtle materials described by Karl (2012)[3] from Uraha (Malawi) suggests that they are food remains, too, but only evidences of class 3 are supported. All fossil specimens are fragmentary; even a most complete shell shows unnaturally widened frontal and caudal openings into the shell. Double colorations in sense of burned turtle bones are hitherto unknown from the Chiwondo Beds. Two bony plates are herewith proposed for discussion as potential tools of *Homo rudolfensis*. This evidence of the consumption of aquatic animals could support an ‘aquatic ape hypothesis’ (Karl, 2012; Morgan, 1997; Verhaegen, 2000; Niemitz, 2006, 2010) [3, 22-25]. They remarkably resemble to scrapers or choppers of wood, flint or bone of other hominid localities. Kaufulub and Stern (1987)[26] describe the attributes and sedimentary context of an assemblage of stone artefacts recovered from Plio-Pleistocene deposits in northern Malawi. The present assemblage was excavated from a paleo-gully layer located within the Homo erectus Beds. It includes flaked pebbles and pebble fragments, flakes, and flake fragments. These currently provide one of the earliest evidence for the presence of hominids in Indonesia and in the whole southern Southeast Asia region. Joordens et al., (2009)[6] investigated a case study based on early Pleistocene Trinil to provide the ecological context and the use of aquatic resources by early hominis (*Homo erectus*) and concluded that the Trinil HK aquatic environment yielded aquatic food resources which could be collected by little or no technology by *Homo erectus*.

3.3 Description of *Duboisemys* n. gen.,

Subclass Testudinata (Klein, 1760), Order Testudines (Batsch, 1788), Infraorder Cryptodira (Cope, 1868), Supra family Testudinoidea (Batsch, 1788), Family Geoemydidae (Theobald, 1868), Genus *Duboisemys* n. gen.

Type species: *Hardella isoclina* Dubois, 1908 [27].

Etymology: The name *Hardella* has no real meaning known; Gray (1870) has either coined a word with no meaning or used an Indian dialect word and Latinized it (Das, I., pers. comm. To HDP). The new name is given in honor to Marie Eugène François Thomas Dubois (1858 – 1940) a Dutch paleoanthropologist and geologist who has been excavated first the *Homo erectus* at Java and its accompanying fauna (the name *Duboisia* R. Br. is preoccupied for a member of the plant family Solanaceae and Dubois santeng or Dubois' antelope *Duboisia* Stremme, 1911); *emys* Greek έμυς - turtle. The species name *isoclina* can be interpreted in two ways to: (1) iso Greek ίσο — same, kline Greek κλίνη — bed, in the sense of the same layer or bed as *Batagur* and *Chitra*, the other two turtle genera in his sample from Trinil; (2) iso Greek ίσο — equal; clina / clinare Latin — to bent, in the sense of a line on a diagram or map connecting points of equal gradient or inclination, which would refer to the shape of the shell.

Plate 2: Photographs of the holotype of *D. isoclina* (Dubois, 1908), NCBN — Dub 2722:
1 - Dorsal view of carapace 2 - Ventral view of plastron.

Plate 3: Photographs of the holotype of *D. isoclina* (Dubois, 1908), NCBN — Dub 2722:
1 - Shell in left lateral view 2 - Shell in right lateral view 3 - Shell in frontal view 4 - Shell in caudal view.

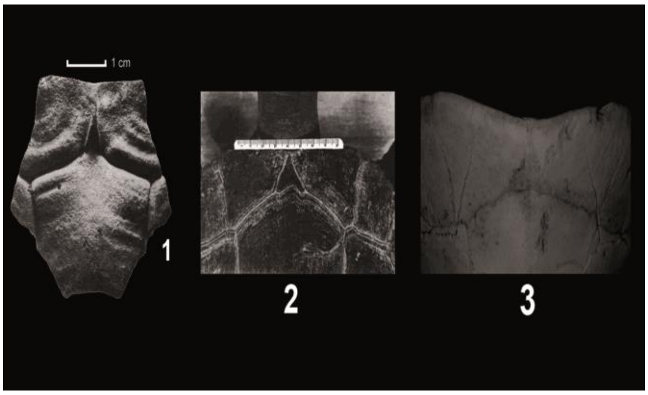

Plate 4: Fig 1-Holotype of synonym *Batagur signatus* (Jaekel, 191I) (MB: R. 5) from Trinil at Java, a nuchal plate of *Orlitia borneensis* (Gray, 1873) (ZMB: 14 168) in compare with a recent specimen of that species from Batano Lupar at Kalimantan (figure 2), according Karl (1987: pl. 13, fig. 2). Remark the absolute same outline of the cervical scute. This is further supported by the identical ratios of the comparison specimen (figure 3) from the turtle project in Leiden (Pritchard-collection 7547). The material appears not to be different from *O. borneensis* in the alleged lacking anteriorly widened mushroom-shaped first vertebral scute (Liat and Das, 1999; Diesmos et al, 2005, Setiyabudi et al 2016).

Duboisemys isoclina (Dubois, 1908) n. comb. - Trinil Pond Turtle

(Plate 2-4)
1908 — *Hardella isoclina* n. sp., p. 1270.
1957 — *Clemmys isoclina*, Williams, p. 235-236.
1964 — *Clemmys isoclina* Kuhn, p. 69, 89.
1997 — *Mauremys isoclina*; Das, p. 72.
2010 — *Mauremys isoclina*; Hoogmoed *et al*, p. 174.
2015 — *Mauremys isoclina*; TEWG, p. 26.

Stratigraphical and geographical range

Kedoeng Panas, Java (Indonesia); Middle Pleistocene, Trinil Beds/Trinil layer, Joordens et al (2009)[6] dated 1,500,000 to 900,000 ybp, and later a shell from the Trinil main bone layer with 0.54 +/- 0.10 and 0.43 +/- 0.05 (Joordens et al., 2015) [28], see also Ingicco et al. (2018)[20].

Diagnosis (Fig. 4; Plate 2-4): Medium size freshwater turtle with conical nuchal scute; neurals I-III 6A; vertebral and pleural keels absent; posterior margin of carapace smooth; very thin cervical scute trapezoid, central scute hexagonal with S-shaped lateral sulci (Plate 1-4), meta-neural I trapezoid, meta-neural II hexagonal with anterior and posterior lateral sides with the same length, paired caudal scutes overlaps the small pygal and meta-neural II; gular area; gular sulcus cross Entoplastron; humero-pectoral sulcus no contact with entoplastron (Plate 1&4); plastral hinge absent; a large inguinal scute present; plastral buttress strong; CL lesser than 0.5 meter.

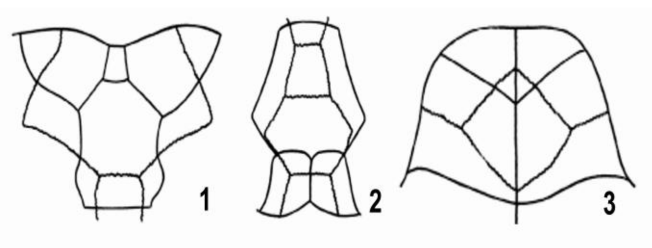

Fig 4: Schematic illustration of the holotype of *D. isoclina* (Dubois, 1908), NCBN — Dub 2722: 1 — nuchal area of carapace, 2 — pygal area of carapace, 3 — frontal lobe of plastron, see also Williams (1957).

Holotype

NCBN — Dub 2722, one shell, holotype (Plates 2-3, 5).

Descriptive reassessment of the holotype: Measurements in the appendix 1. The shell proportions correspond to those of high aquatic river turtles (Moll and Moll 2004)[29], e.g. *Batagur sp*. *Callagur sp*. and *Orlitia sp*. The shell is relatively wide (LWI — 1.4) and high (LHI — 2.3). The bridge is of medium length (BI — 3.06), almost a third of the carapace. The shell surface is smooth, granulated only blurred and bridges keels are not formed. The horn shield sulci are shallow. Missing sutures between neural-and pleural plates areas (Ankyloses) at some places the middle body section are artificially influenced by scratching. The shell was up of many individual parts and retouched in a few places. Some parts are missing in the area of the right inguinal buttress and the posterior lobe of plastron. Over the whole shell small superficial, shallow, speckled bone erosions are distributed. From the visceral points of contact of the iliac bones of pubis through the shell to dorsal two complete perforations are present. These may be caused by fistulae, abnormal connections between two epithelialized surfaces as result from an infection or inflammation, possibly of the ovaries. The slightly convex plastron is characteristic of females, as in the present specimen also. The flat damages on the dorsal side may causes of epibionts like green algae (Fulse, 1976)[30] and are more likely to have a chronic character or affecting their host not drastically.

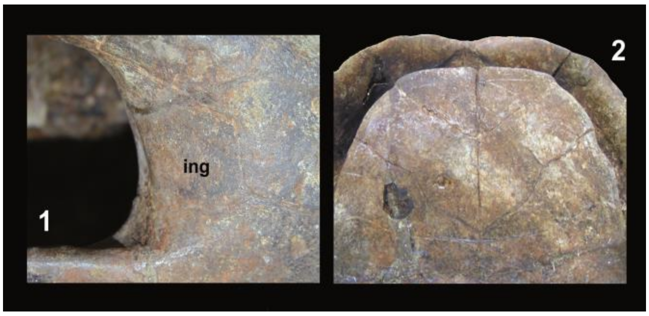

Plate 5: Photographs of the holotype of *D. isoclina* (Dubois, 1908), NCBN — Dub 2722:
1 - Left inguinal region of bridge shows the inguinal scute (ing)
2 - Frontal part of shell in ventral view.

Plate 6: Photographs of one of the most complete fossil carapace and plastron of *Batagur affinis affinis*/ SRQW/ IQPW Geol 1338 from Bogmi Aloi at Java ex. coll. Dr. Bergmann, Weimar;
1 – Carapace in dorsal view, 2 – Plastron in ventral view, 3 – Shell in lateral view from the left, 4 – Shell in anterior view, 5 – Shell in posterior view; (Photography by Thomas Korn, Weimar).

4. Discussion

The character analysis showed an independent position of the family Geoemydidae. Recent molecular phylogenetic studies have revealed that the Geoemydinae and the Batagurinae are polyphyletic. These results indicate that some of synapomorphic characters (e.g., development of the triturating surface) supported Geoemydinae and Batagurinae have independently acquired (i.e., morphological convergence; homoplasy) in several lineages of this family. Therefore a new name for the taxon, *Duboisemys* n. gen. is proposed, and applied with the term *Duboisemys isoclina* (Dubois, 1908) [27] n. comb. The species is a member of the Trinil‘s fauna (Joordens et al. 2009) [6], considered to be from 1,500,000 to 900,000 ybp. The cladistics analyses with comparable fossil and recent geoemydid taxa proved the following relations:

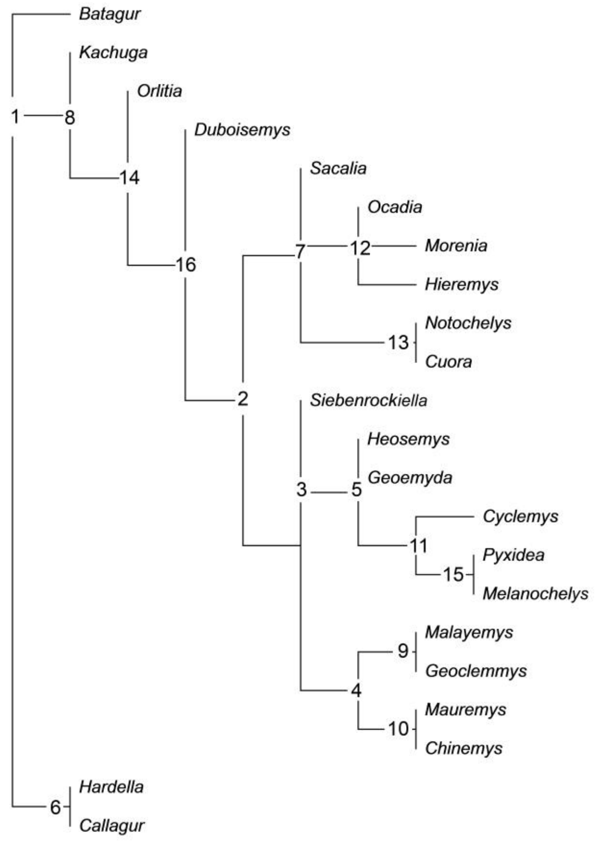

Fig 5: Relationship of *Duboisemys* and Recent Southeast Asian Batagurines: Tree one by PARS©Joseph Felsenstein graphically represented with TreeView©Roderic.

4.1 Relationship of Duboisemys and recent Southeast Asian Batagurines (Figure 5 - 7): According to the present diagnostic analysis (See Appendix 2), features of *Kachuga, Orlitia, Duboisemys* n. gen., *Sacalia* and *Siebenrockiella* show taxa with relative autonomy. Genera pairs are *Notochelys* and *Cuora*, *Heosemys* and *Geoemyda, Malayemys* and *Geoclemys* and *Mauremys* and *Chinemys.* End groups / branches of the tree are *Ocadia* / *Morenia* / *Hieremys; Pyxidea / Melanochelys / Cyclemys* and *Hardella / Callagur / Batagur*. This division mainly reflects the situation in other analyzes of different premises, and also reflects a high degree of safety within our results. This is true for morphological studies (Hirayama, 1984) [31] as well as for genetic studies (Barth et al., 2003; Feldman and Parham 2004; Guillon et al., 2012; Minh et al., 2007; Spinks et al., 2004 and Thomson and Shaffer 2010) [32-37].

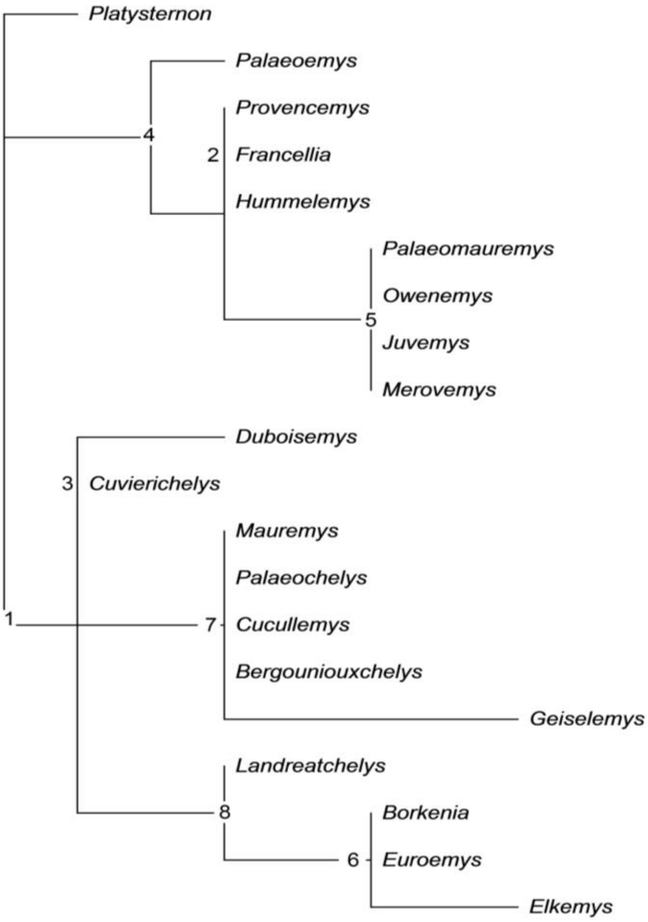

Fig 6: Relationship of *Duboisemys* and fossil *Eurasian Batagurines*: Tree two by PARS©Joseph Felsenstein graphically represented with TreeView©Roderic.

4.2 Relationship of *Duboisemys* and fossil Eurasian Batagurines (Figure 6):
The monophyletic Ptychogasteridae (Ptychogastrini) include after Hervet (2004b)[16] the genera *Echmatemys*, *Hummelemys*, *Geiselemys*, *Ptychogaster* and *Clemmydopsis*, and are autapomorph characterized by a strong and long dorsal extensive epiplastral lip with two lateral "Ptychogasterid spikes". At the same time these are plesiomorphic characters compared to the corresponding features of the original Testudinoidea. This apomorphies are pronounced since the basis of Ptychogastrini. Sometime later, they also appeared as homoplasies at the Palaeochelyinae. The advanced compared to the Costalia / Vertebralia of Palaeomauremys and *Mauremys* have been acquired independently in terms of homoplasy by Hervet (2004a, 2003)[15&38]. *Geiselemys* is the only taxon of this group, which is used in the present analysis. Karl and Wettlaufer (2011)[39] erected the subfamily Palaeochelyinae for the so-called "*Palaeochelys-Mauremys*-complex". These include the following genera *Palaeoemys*, *Francellia*, *Juvemys*, *Owenemys*, *Euroemys*, *Borkenia*, *Landreatchelys*, *Cuvierichelys*, *Bergouniouxchelys*, *Cucullemys*, *Provencemys*, *Palaeochelys*, *Palaeomauremys* (syn. *Promalacoclemys*) and *Mauremys*. Claude and Tong (2004)[40] and Danilov et al. (2017)[41] took the majority of this name in the synonymy of *Palaeoemys*, which in turn to

the so called *Malayemys*-complex belongs, with *Geoclemys*, *Malayemys*, and *Borkenia*. *Mauremys* belongs to the *Melanochelys*-complex with *Sacalia, Cuora, Cistoclemmys, Notochelys, Heosemys, Hieremys, Cyclemys, Leucocephalon, Ocadia, Chinemys, Palaeochelys, Siebenrockiella* and *Geoemyda.* According to Danilov et al. (2017) [41] enclose the *Batagur* complex (*Batagur, Callagur, Chinemys, Hieremys, Kachuga, Malayemys, Ocadia*), the *Hardella* complex (*Geoclemys*, *Hardella, Morenia*), the *Orlitia* complex (*Orlitia, Siebenrockiella*) and the *Geoemyda* complex (*Cuora, Cyclemys, Geoemyda, Heosemys, Mauremys, Melanochelys, Notochelys, Rhinoclemys, Sacalia*) into recent Geoemydidae. The genetic tests of Batagurid turtles have resulted in unification in several morphologically and structural forms with the lumping genus *Mauremys* (Fritz and Havas, 2007)[42]. They described that *Sacalia* and *Ocadia* synonyms of *Mauremys* etc., of which *Mauremys caspica* and *M. rivulata* show a significant eastward expansion of the areas (Fritz et al 2007)[42]. Here are the recent genera names are used, since these are assigned to morphological well defined characteristics, to fossil taxa see also Karl (2013)[43] and Karl et al (2012) [44].

Dubois (1908)[27] very briefly diagnosed a new species of emydine turtle, *Hardella isoclina*, from the Trinil Beds in Java. The holotype and sole example of this fossil turtle species is held at "Netherlands Centre for Biodiversity “Naturalis". The very fine unique type shell has never been figured or fully described, the generic assignment appears to be incorrect, and the original diagnosis is insufficient. The fossil is a very distinct species and a very noteworthy component of the Trinil’s fauna but even after much study and comparison it proves impossible to refer it with confidence to any known genus, and in the absence of any knowledge of the characters of the skull no new genus can be satisfactorily defined. The Trinil’s form appears to resemble most closely the living species *Mauremys mutica* from southern China, Formosa, Hainan, and Japan. The extant species of this genus is *Hardella thurjii* is restricted to flood plains of Indus river (Pakistan) and Gangas and Brahamputra (India) Das (1997)[45]. *Hardella thurjii* (Brahminy river turtle) and *Pangshura tecta* of hard shelled turtles (Geoemydidae) were recorded as rare in District of Charsadda in Pakistan (Safi and Khan, 2014)[46] compared Dubois with a variety of South-East and East Asian turtles. But current study revealed that *Duboisemys* is much closer to East Asian turtle, *Orlitia* than to the other compared genera, which were already described from the *Homo erectus*-layers, so that it must be understand as member of the *Orlitia* complex (Figure 5). In the comparison of the plates 1-3 with plate 4 the absolutely different character of the shell structure between both Javanian geoemydid species *Duboisemys isoclina* and *Batagur affinis affinis* appears. Remains of femora, rigth tibia and fibula from the type materials of *Desmemys bertelsmanni* rediscovered, described and figured as lectotype by Karl and Safi (2019)[47]. This type of sample is discussed and elucidated on geographically and strati-graphically comparable material as *Duboisemys* of current studies.

APPENDIX I

Measurements of Shell of *Duboisemys isoclina* (Dubois, 1908) in mm

Carapace length	314
Carapace width	223,5
Shell hight	138,5
Bridge length sin	103,64
Bridge length dex	101,79

Carapace

Dub 2722	b_{ant}	b_{post}	$l_{ant\ sin}$	$l_{ant\ dex}$	$l_{post\ sin}$	$l_{post\ dex}$	l_{med}	b_{max}
N I	**22**	**23,45**	**17**			**17,62**		
N II	**22,65**	**19,76**	**8,2**			**27,42**		
N III	**23,7**	**19,83**	**8,62**			**27,47**		
N IV	**19,41**	**26,69**	**7,58**			**21,84**		
N V		**25,79**		**4,43**		**24,31**		
N VI	**25,75**	**24,76**	**16,51**	**7,25**		**15,11**		
N VII	**24,75**	**20,45**	**7,81**		**9,43**	**15,33**		
N VIII	**20,46**	**16,23**	**9,49**	**9,54**	**15,58**	**15,333**		
MN 1	**16,23**		**24,78**					
MN 2		**53,04**	**19,34**			**30,85**		**64,74**
Pygale	**53,04**	**39,74**	**23,96**	**24,68**			**21,78**	

Plastron

	l	b
Frontal lobe	75	129,93
Caudal lobe	86,49	126,48

Gular thickness	14,54
Anal thickness	8,52
Entoplastron length	50,12
Entoplastron width	53,91
Gular sulcus at entoplastron	2
Pectoral sulcus to entoplastron	5

APPENDIX II

PARS (Discrete character parsimony) is a Wagner parsimony method and generates Steiner minimum tree. The most recent edition 3.69 (Felsenstein 1986) was used. The graphic transformation of the trees was generated via TreeView©Roderic Page (Page 1996).

Character coding: 1 — cervical scute conical (1) or parallel sided (0); 2 — vertebral keels present (1) or absent (0); 3 — pleural keels present (1) or absent (0); 4 — gular sulcus cross entoplastron present (1) or absent (0); 5 - humeropectoral sulcus cross entoplastron present (1) or absent (0); 6 — posterior margin of carapace strongly serrated (1) or smooth (0); 7 — plastral hinge present (1) or absent (0); 8 — plastral buttress strong (1) or moderate (0); 9 — neurals I-III 6A present (0) or another (1); 10 — maximum carapace length over 0.5 meter (1) or lesser (0).

Character analysis 1 (Figure 6)

Data matrix: *Batagur* 010000111; *Callagur* 111000111; *Chinemys* 111100110; *Cuora* 110101110; *Cyclemys* 110111000; *Geoclemmys* 111010110; *Geoemyda* 111110000; *Hardella* 111000111; *Heosemys* 111110000; *Hieremys* 100100000; *Kachuga* 110010111; *Malayemys* 111010110; *Mauremys* 111100110; *Melanochelys* 111111100; *Morenia* 100000010; *Notochelys* 110101110; *Ocadia* 100100010; *Orlitia* 110010011; *Pyxidea* 111111100; *Siebenrockiella* 111110010; *Sacalia* 110100010; *Duboisemys* 110010010.

Tree by PARS©Joseph Felsenstein:

(*Kachuga*:0.00,(*Orlitia*:0.00),(*Duboisemys*:0.00),(*Sacalia*:0.00),(*Ocadia*:0.00,*Morenia*:1.00,*Hieremys*:1.00):1.00,(*Notochelys*:0.00,*Cuora*:0.00)(:2.00):1.00,(*Siebenrockiella*:0.00),(*Heosemys*:0.00,*Geoemyda*:0.00),(*Pyxidea*:0.00), (*Melanochelys*:0.00):1.00,*Cyclemys*:1.00):1.00):1.00,((*Malayemys*:0.00,*Geoclemmys*:0.00):1.00,(*Mauremys*:0.00,*Chinemys*:0.00):1.00):1.00):1.00):1.00):1.00):1.00):1.00,(*Hardella*:0.00,*Callagur*:0.00):1.00,*Batagur*:0.00)[0.0250].

Character analysis 2 (Figure 7)

Data matrix: *Platysternon* 0001000010 (outgroup); *Elkemys* 0100000010; *Hummelemys* 1101000010; *Merovemys* 1111000010; *Geiselemys* 1001101000; *Palaeoemys* 0101000010; *Francellia* 1101000010; *Juvemys* 1111000010; *Owenemys* 1111000010; *Euroemys* 1100000010; *Borkenia* 1100000010; *Cuvierichelys* 1001000010; *Bergouniouxchelys* 1001100010; *Cucullemys* 1001100010; *Provencemys* 1101000010; *Landreatchelys* 1000000010; *Palaeochelys* 100??00010; *Palaeomauremys* 1111000010; *Mauremys* 1001100010; *Duboisemys* 1001000110.

Tree by PARS©Joseph Felsenstein — (*Palaeoemys*:0.50,(*Provencemys*:0.00,*Francellia*:0.00,(*Palaeomauremys*:0.00,*Owenemys*:0.00,*Juvemys*:0.00,*Merovemys*:0.00):1.00,*Hummelemys*:0.00):0.50):1.00,(*Duboisemys*:1.00,*Cuvierichelys*:0.00,(*Mauremys*:0.00,*Palaeochelys*:0.00,*Cucullemys*:0.00,*Bergouniouxchelys*:0.00,*Geiselemys*:2.00):1.00,(*Landreatchelys*:0.00,(*Borkenia*:0.00,*Euroemys*:0.00,*Elkemys*:1.00):1.00):1.00):0.50,*Platysternon*:0.50)[0.0227].

APPENDIX III

Referred fossil specimens

Bangle, Java: *Batagur baska*/ RMNH 579/ plastron, RMNH 590/ carapace, RMNH 594/ carapace and plastron remain.

Bogmi Aloi, Java: *Batagur affinis affinis*/ SRQW/ IQPW Geol 1338/ carapace and plastron, ex. Coll. Dr. Bergmann, Weimar (plate 4, fig. 1-5).

Kebon Doeren, Java: *Batagur affinis affinis*/RMNH 10378/ carapace/ plastron remains, RMNH 10937/ carapace/ plastron remain.

Kedoeng Broeboes, Java: *Batagur affinis affinis*/ RMNH 5521/ carapace and plastron remains, RMNH 9211/ plastron remain, RMNH 9212/ plastron remain, RMNH 9935/ carapace remain, RMNH 9943/ plastron remain, RMNH 9943C/ plastron remain, RMNH 10186/ plastron remain, RMNH 10377/ carapace/ plastron remains, RMNH 10947/ carapace/ plastron remains, RMNH 10948/ carapace/ plastron remains, RMNH 15557/ carapace/ plastron remains.

Kedoeng Panas, Java: *Hardella isoclina* holotype/ RMNH 2722/ carapace/ plastron; *Batagur baska*/ RMNH 2700/ carapace and plastron remains, RMNH 2701/ carapace and plastron remains, RMNH 2702/ carapace and plastron remains, RMNH 2703/ carapace and plastron remains, RMNH 9874/ carapace, RMNH 9875/ carapace/ plastron, RMNH 9876/ carapace/ plastron, RMNH 9877/ carapace/ plastron, RMNH 9878/ carapace/ plastron.

Trinil, Java: *Batagur affinis affinis*/ RMNH 2672A/ carapace and plastron remains, RMNH 2673/ carapace remain, RMNH 2674/ carapace and plastron remains, RMNH 2675/ carapace and plastron remains, RMNH 2676/ carapace and plastron remains, RMNH 2677/ carapace and plastron remains, RMNH 2704/ carapace remain, RMNH 2705/ carapace remain, RMNH 2720/ plastron, RMNH 2721/ carapace remain, RMNH 2723/ plastron, RMNH 2738/ carapace remain, RMNH 2739/ carapace remain, RMNH 2740/ carapace, RMNH 2741/ carapace, RMNH 2742/ carapace remain, RMNH 2743/ carapace remain, RMNH 2751/ carapace/ plastron, RMNH 2752/ carapace, RMNH 2704/ carapace remain, RMNH 2705/ carapace remain, RMNH 2720/ plastron, RMNH 2721/ carapace remain, RMNH 2723/ plastron, RMNH 2738/ carapace remain, RMNH 2739/ carapace remain, RMNH 2740/ carapace, RMNH 2741/ carapace, RMNH 2742/ carapace remain, RMNH 2743/ carapace remain, RMNH 2751/ carapace/ plastron, RMNH 2752/ carapace, RMNH 4217/ carapace remain, RMNH 4398/ carapace remain, RMNH 4442/ carapace and plastron remains, RMNH 4443/ carapace and plastron remains, RMNH 4444/ carapace and plastron remains, RMNH 4462/ carapace and plastron remains, RMNH 4463/ carapace and plastron remains, RMNH 4464/ carapace and plastron remains, RMNH 4465/ carapace and plastron remains, RMNH 4466/ carapace and plastron remains, RMNH 4585/ carapace, RMNH 6679/ plastron remain, RMNH 6680/ plastron remain, RMNH 8533/ carapace remain, RMNH 9225/ plastron remain, RMNH 9371/ plastron remain, RMNH 9372/ carapace remain, RMNH 9397/ plastron remain, RMNH 9398/ plastron remain, RMNH 9867/ plastron, RMNH 9868/ carapace, RMNH 9869/ carapace, RMNH 9870/ carapace, RMNH 9871/ carapace, RMNH 9872/ carapace, RMNH 9873/ plastron, RMNH 9879/ carapace and plastron remains, RMNH 9880/ carapace and plastron remains, RMNH 9881/ carapace remain, RMNH 9882/ carapace remain, RMNH 9883/ carapace remain, RMNH 9884/ carapace remain, RMNH 9887/ plastron, RMNH 9888/ carapace remain, RMNH 9889/ carapace remain, RMNH 9890/ plastron, RMNH 9891/ carapace remain, RMNH 9892/ carapace, RMNH 9893/ plastron, RMNH 9894/ carapace remain, RMNH 9895/ carapace remain, RMNH 9896/ carapace remain, RMNH 9897/ carapace remain, RMNH 9898/ carapace remain, RMNH 9899/ carapace remain, RMNH 9900/ carapace remain, RMNH 9901/ carapace remain, RMNH 9902/ carapace remain, RMNH 9903/ carapace remain, RMNH 9904/ carapace remain, RMNH 9905/ carapace remain, RMNH 9906/ carapace remain, RMNH 9907/ carapace remain, RMNH 9908/ carapace remain, RMNH 9909/ plastron, RMNH 9910/ plastron, RMNH 9911/ carapace, RMNH 9912/ plastron, RMNH 9913/ carapace remain, RMNH 9914/ carapace, RMNH 9915/ plastron remain, RMNH 9916/ plastron, RMNH 9917/ carapace, RMNH 9918/ carapace remain, RMNH 9919/ plastron, RMNH 9920/ plastron remain, RMNH 9921/ carapace, RMNH 9922/ carapace remain, RMNH 9923/ carapace remain, RMNH 9924/ carapace remain, RMNH 9925/ carapace remain, RMNH 9926/ carapace remain, RMNH 9927/ plastron remain, RMNH 9928/ carapace/ plastron remains, RMNH 9929/ plastron remain, RMNH 9930/ plastron remain, RMNH 9931/ plastron remain, RMNH 9932/ carapace, RMNH 9933/ carapace/ plastron remains, RMNH 9934/ carapace remain, RMNH 9947/ carapace remain, RMNH 9949/ plastron remain, RMNH 9950/ plastron, RMNH 9950A/ carapace/ plastron remains, RMNH 9951/ carapace/ plastron, RMNH 9952/ plastron, RMNH 9954/ carapace/ plastron, RMNH 9955/ carapace/ plastron, RMNH 9956/ carapace/ plastron, RMNH 10120/ carapace remain, RMNH 10121/ plastron, RMNH 10122/ plastron, RMNH 10123/ plastron, RMNH 10124/ plastron, RMNH 10125/ carapace remain, RMNH 10127B/ carapace remain, RMNH 10189/ plastron remain, RMNH 10190/ plastron, RMNH 10191/ carapace, RMNH 10366/ plastron remain, RMNH 15565/ carapace/ plastron remains, RMNH 15566/ carapace remains, RMNH 15567/ carapace remains, RMNH 15568/ carapace/ plastron remains.

Pramesan, Java: *Batagur affinis affinis*/ RMNH 555/ plastron remain, RMNH 10379/ carapace/ plastron remains, RMNH 10380/ carapace/ plastron remains.

Java: *Batagur affinis affinis*/ RMNH 473/ plastron remain, RMNH 568/ plastron remain, RMNH 2699/ plastron, RMNH 10337/ carapace/ plastron remains, RMNH 10338/ carapace/ plastron remains, RMNH 10339/ carapace/ plastron remains, RMNH 10340/ carapace/ plastron remains, RMNH 13554/ carapace/ plastron remains, RMNH 13606/ carapace/ plastron remains, RMNH 15553/ carapace remain, RMNH 15554/ carapace remain, RMNH 15554/ carapace remain, RMNH 15555/ carapace remain, RMNH 15556/ carapace remain, RMNH 15558/ carapace remain, RMNH 15559/ plastron remain, RMNH 15560/ carapace remain, RMNH 15561/ plastron remain, RMNH 15562/ plastron remain, RMNH 15563/ plastron remain, RMNH 15564/ plastron remain, RMNH 15575/ carapace remain, RMNH 15576/ carapace remain, RMNH 15577/ carapace remain, RMNH 15578/ plastron remain; *Batagur affinis affinis*/ MB R. 3/ *Batagur siebenrocki* neotype/ carapace and plastron; *Orlitia borneensis*/ MB R. 5/ *Batagur signatus* holotype/ nuchal plate (plate 5, fig. 1).

Referred recent specimens

Batagur baska: CP 4928/ coll. Pritchard/ bony carapace and plastron/ Perak, Malaysia.

Callagur borneoensis: CP 3392/ coll. Pritchard/ bony carapace and plastron/ Malaysia; CP 6499/ coll. Pritchard/ bony carapace and plastron/ Perak, Malaysia; RMNH.RENA.3296 (Naturalis Leiden)/ whole organism in alcohol/ Borneo.

Cuora ambionensis: CP 318/ coll. Pritchard/ bony carapace and plastron/ without locality data.

Cyclemys dentata: CP 7490/ coll. Pritchard/ bony carapace and plastron/ without locality data; - CP 5244/ coll. Pritchard/ bony carapace and plastron/ without locality data.

Heosemys grandis: CP 7543/ coll. Pritchard/ carapace and plastron/ without locality data.

Heosemys spinosa: RMNH.RENA.3837 (Naturalis Leiden)/ whole organism in alcohol/ Sumatra; CP 6601/ coll. Pritchard/ bony carapace and plastron/ Malaysia; CP 6602/ coll. Pritchard/ bony carapace and plastron/ Malaysia.

Hieremys annandalei: CP 5453 (large = 3804)/ coll. Pritchard/ carapace and plastron/ without locality data.

Malayemys subtrijuga: CP 3231/ coll. Pritchard/ bony carapace and plastron/ Hanoi, Vietnam; CP 3447/ coll. Pritchard/ bony carapace and plastron/ Hanoi, Vietnam.

Notochelys platynota: CP 3650/ coll. Pritchard/ bony carapace and plastron/ Penang, Malaysia.

Siebenrockiella crassicollis: CP 2508/ coll. Pritchard/ bony carapace and plastron/ without locality data; CP 11/ coll. Pritchard/ bony carapace and plastron/ without locality data.

APPENDIX IV

Referred type specimens from Trinil according Jaekel (1911), investigated by Karl (1983), See Plate 7:

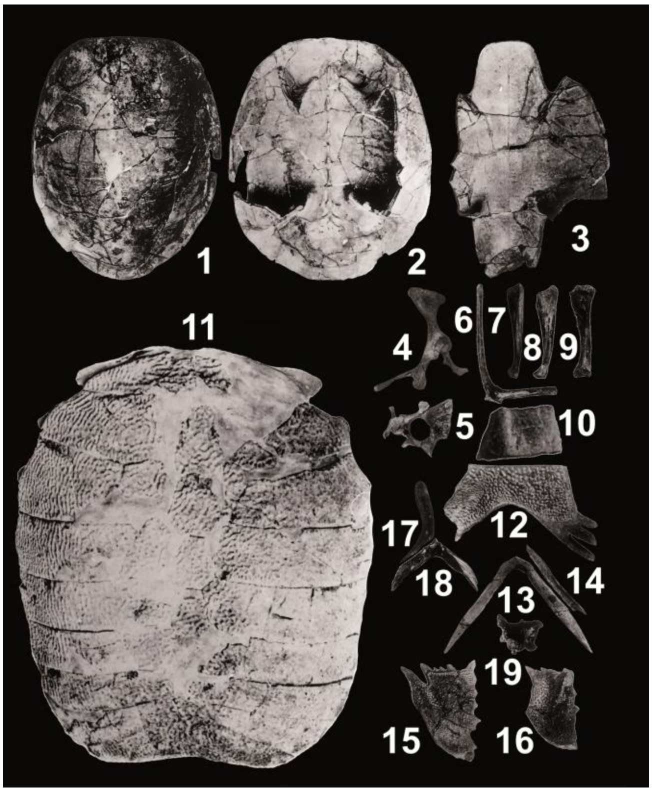

Plate 7: Type specimens to *Batagur Siebenrocki* (destroyed during WW II according Dr. K. Fischer); 1- carapace dorsal view, 2- carapace visceral view, 3- plastron visceral view, 4-5- pelvis remains; 6- scapula, 7-8- coracoids, 9-radius; type specimen to *Batagur signatus*, see also plate 4-1, 10-peripherale; type specimens to *Chitra Selenkae*: 11- Carapace (Complete view), 12- left hypoplastron, 13- entoplastron, 14- epiplastron remain, 15- right xiphiplastron; type specimen to *Chitra minor*, 16- right xiphiplastron; type specimens to *Trionyx trinilensis*, 17- entoplastron, 17- left epiplastron, according Jaeckel (1911).

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Statement of Conflict of Interest

The Authors declare no conflict of interest

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