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Phylogenetic Relationships Within the Batagur Complex (Testudines: Emydidae: Batagurinae)

Jean M. Capler

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Phylogenetic Relationships Within The Batagur Complex

(Testudines: Emydidae: Batagurinae)

(TITLE)

BY

Jean M. Capler

THESIS

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PHYLOGENETIC RELATIONSHIPS WITHIN THE
BATAGUR COMPLEX (TESTUDINES: EMYDIDAE: BATAGURINAE)

ABSTRACT

Relationships between 10 species of the batagurine genera Batagur, Callagur, Kachuga, Hardella, and Morenia are discussed based on a cladistic analysis of 35 morphological characters. Ocadia sinensis (Emydidae: Batagurinae) was used as the outgroup species. Four cladograms were produced with a length of 59.0 steps and a 0.75 consistency index. In contrast with previous studies, Hardella and Morenia do not appear as a monophyletic clade. Instead, Hardella is included with the remaining ingroup taxa (exclusive of Morenia) based on five synapomorphies. The present genus Kachuga was determined to be paraphyletic, having excluded the present genera Batagur and Callagur. The pangshura subgroup of the genus (consisting of the smaller members of the genus -- K. smithi, K. tecta, and K. tentoria) is distinguished by six synapomorphies and appears to be a sister group of the clade formed by an unresolved polychotomy including Batagur, Callagur, and the kachuga subgroup (consisting of the larger members of the genus -- K. dhongoka, K. kachuga, and K. trivittata). Batagur and Callagur are included with the kachuga subgroup based on two synapomorphies. A possible taxonomic revision suggested is to elevate the pangshura group to generic rank and include Batagur, Callagur, and the remaining Kachugas as a separate genus Batagur.

Dedicated to the memory of my mom,
who taught me to love the natural world around me,
and to my dad,
who taught me to believe in myself.
I love you both.

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INTRODUCTION

Historical Overview

Relationships of the subfamily Batagurinae (Emydidae: Testudines) have proven problematic due to the paucity of material available for study and the apparent high degree of homoplasy in the group. In his classic paper on the taxonomy of emydid turtles published in 1964, McDowell partitioned the family Emydidae into two subfamilies, the predominately New-World Emydinae and the predominately Old-World Batagurinae. However, later workers (Hirayama, 1984; Gaffney and Meylan, 1988) have suggested that McDowell's Batagurinae may be polyphyletic. Hirayama (1984) divided the subfamily into a primary palate group and a secondary palate group, the latter forming a clade with the Testudinidae. The secondary palate group corresponds to McDowell's "broad triturating surface" group, including his *Hardella*, *Batagur*, and *Orlitia* (sic) Complexes. Based on Hirayama's work, Gaffney and Meylan (1988) proposed that McDowell's Emydinae, Batagurinae, and Testudininae should be elevated to family rank, with the newly formed "Bataguridae" comprising two subfamilies (Batagurinae and Geoemydinae).

McDowell (1964) introduced the designation Batagur complex to include species of the genera Batagur, Callagur, Kachuga, Ocadia, Hieremys, Malayemys, and Chinemys, all members of Hirayama's secondary palate group and Gaffney and Meylan's Batagurinae. Loveridge and Williams (1957) previously had suggested Morenia was a close relative as

(1984), Moll (1986), and Gaffney and Meylan (1988) suggests that only Batagur, Callagur, and Kachuga, along with Hardella and Morenia represent a monophyletic lineage. Relationships within this complex group, especially within the Kachuga, require resolution.

Over the taxonomic history, the Kachuga have been considered as: 1.) a monophyletic genus comprised of two subgenera, Kachuga and Pangshura (Gray, 1855; Moll, 1986); 2.) a monophyletic genus comprised of two distinct species groupings -- one comprised of larger riverine species K. trivittata, K. kachuga, and K. dhongoka and a second which included the smaller, lotic-adapted K. smithi, K. tecta, K. tentoria, and K. sylhetensis (McDowell, 1964); 3.) a monophyletic genus without species groupings (Boulenger, 1889, 1890); and 4.) two separate genera Pangshura and Kachuga (Gunther, 1864; Gray, 1869).

The situation is further complicated when the positions of Callagur and Batagur are also considered. McDowell noted the close relationship between K. kachuga, K. trivittata, and Callagur, suggesting that they might be considered a single superspecies. He suggested no affinity between Batagur and the rest of this complex. However, Hirayama (1984) hypothesized and Gaffney and Meylan (1988) accepted that Batagur and Callagur, Hardella and Morenia, and Kachuga formed three separate monophyletic sister groups. The availability of an extensive collection of batagurine genera at Eastern Illinois University provided an excellent opportunity to clarify the relationships among

the aforementioned genera and to determine the status of the kachuga and pangshura lineages.

Species Accounts

Ocadia sinensis (Gray, 1834)

The Chinese striped-neck turtle, is an herbivorous species found in Taiwan, southern China, and northern Vietnam. It lacks seasonal and sexual dichromatism and attains a maximum carapace length of 24 cm. Ocadia is restricted to lowland, lentic habitats (Pritchard, 1979; Ernst and Barbour, 1989).

Morenia petersi (Anderson, 1876)

The Indian eyed turtle is distributed in northeastern India and Bangladesh. It reaches a maximum carapace length of 20 cm, does not exhibit seasonal or sexual dichromatism, and inhabits slow-moving rivers, pond, and swamps. Little else is known of its natural history (Pritchard, 1979; Moll and Vijaya, 1986; Ernst and Barbour, 1989).

Morenia ocellata (Dumeril and Bibron, 1835)

The Burmese eyed turtle is found only in southern Burma. Slightly larger than M. petersi, this species attains a maximum carapace length of 22 cm. M. ocellata also lacks seasonal and sexual dichromatism. It is found in slow-moving rivers, ponds, and swamps as well as some ephemeral habitats (Pritchard, 1979; Ernst and Barbour, 1989).

Hardella thurjii (Gray, 1831)

The Crowned river turtle inhabits ponds, slow-moving rivers, and oxbow lakes in Pakistan, northern India, Nepal, and Bangladesh (Iverson, 1992). This species is primarily herbivorous (Das, 1991) and does not exhibit seasonal or sexual dichromatism. Females may reach 61 cm in shell length, while males reach only 18 cm. Nesting occurs in Bangladesh at the beginning of the monsoons (Khan, 1987). Females may travel 50 m to one kilometer inland to nest in sandy soil around bushes (Vijaya and Manna, 1982) or on sand banks (Khan, 1987). Uncommon but widespread in the Indus and Ganges drainages, Hardella is heavily exploited in the markets (Moll, 1983).

Callagur borneoensis (Schlegel and Muller, 1844)

The Painted terrapin ranges from south Thailand through Malaysia, Sumatra, and Borneo (Moll, 1985; Iverson, 1992). This primarily herbivorous species exhibits marked seasonal and sexual dichromatism (Moll, 1980; Moll, et al., 1981; Moll, 1985). Maximum carapace length is 50 cm in females and 40 cm in males (Moll, 1985). This species inhabits estuaries of moderate to large sized rivers. During the reproductive season, females lay 10-12 eggs in shallow sand nests on sea beaches within two kilometers of the mouth of their home river. In Malaysia, nesting occurs from June to August on the East Coast and from October to January on the West Coast (Moll, 1980). While adults are generally not threatened by humans, the eggs are

overexploited for food, a practice which has created a serious decline in populations (Moll, 1980).

Batagur baska (Gray, 1831 "1830-1835")

The River terrapin occurs from India and Bangladesh eastward to Vietnam, including the Malay Peninsula and Sumatra (Moll, 1978, 1980, 1985; Iverson, 1992). This chiefly herbivorous species also exhibits seasonal and sexual dichromatism. Females may exceed 60 cm in shell length, while males attain a maximum size of 49 cm. Throughout most of the year, Batagur baska inhabits the estuarine regions of rivers, but during the dry season, females migrate up-river to lay an average of 26 eggs in nests on sandy banks of rivers from November to April depending on the location (Moll, 1978, 1985). This species has seriously declined in numbers due to habitat destruction, overexploitation of eggs, and the use of adults for food (Moll, 1978, 1985).

Kachuga kachuga (Gray, 1831 "1830-35")

The Red-crowned roofed turtle occurs in northern India, southern Nepal, and Bangladesh (Iverson, 1992). It is thought to be primarily herbivorous, based on food habits observed in captivity (Moll, 1986). Maximum carapace length reported is 56 cm (Moll, 1986; Das, 1991), with females larger than males. Seasonal and sexual dichromatism is striking (Moll, 1986; Das, 1991). This species inhabits moderate to large rivers, and nesting occurs primarily on sand banks in March and April (Moll,

1986). A relatively rare turtle which is sometimes exploited for its flesh, it is protected under Schedule I of the Indian Wildlife (Protection) Act of 1972. In an effort to increase the reproductive success of the species, wild-laid clutches are collected and reared in a hatchery in the Chambal region of central India (Das, 1991).

Kachuga dhongoka (Gray, 1834)

The Three-striped roofed turtle ranges through northern India, Nepal, and Bangladesh (Iverson, 1992). Initially reported to be herbivorous by Anderson (1876) based on captive feeding behavior, it is now known that males are omnivorous (Moll, 1986). The diet of females is unknown. Females attain 48 cm shell length, while males reach only 26 cm (Das, 1991). Found in moderate to large rivers, K. dhongoka nests on sand banks. Peak nesting season is in March and April (Moll, 1986; Das, 1991). Heavily exploited for its flesh, the numbers of three-striped roofed turtles are rapidly declining (Das, 1991).

Kachuga trivittata (Dumeril and Bibron, 1835)

The Burmese roofed terrapin inhabits both the tidal and up-river portions of the Irrawaddy and Salween Rivers in Burma (Theobald, 1868; Smith, 1931, Pritchard, 1979). This herbivorous species exhibits both sexual dichromatism and dimorphism. Females reach 60 cm shell length while males do not exceed 50 cm (Theobald, 1868). Nesting occurs in January and February on the sand banks of rivers

(Theobald, 1868; Smith, 1931). Although the eggs have been exploited in the past (Theobald, 1868), little is known of the present population levels (Moll, 1985).

Kachuga smithi (Gray, 1863)

The Brown roofed turtle inhabits the Indus and Ganges-Brahmaputra drainages in Pakistan, northern India, Nepal, and Bangladesh (Iverson, 1992). Two subspecies are recognized: the heavily pigmented brown-roofed turtle, K. s. smithi (Gray, 1863) from the Indus and Ganges River systems in Pakistan, India, and Bangladesh, and the more lightly pigmented pale-footed roofed turtle, K. s. pallidipes (Moll, 1987), from the northern tributaries of the Ganges River in India and Nepal. Das (1985), Minton (1966), and Smith (1931) report this species to be omnivorous with a carnivorous bias, but Moll (1987) found only plant material in the gut contents of a subadult female. Females are larger than males, attaining a maximum shell length of 23 cm (Das, 1991). The brown-roofed turtle generally occurs in both lotic and lentic riverine habitats (Moll, 1987; Das, 1991), sexual dichromatism is lacking (Moll, 1986), and peak nesting occurs from late August to mid-November (Das, 1991). This species is uncommon, and further studies must be conducted to determine what conservation efforts are required to preserve it (Das, 1991).

Kachuga tentoria (Gray, 1834)

The Indian tent turtle is distributed in Peninsular

India, Bangladesh (Moll, 1987; Iverson, 1992), and Nepal (Moll, 1987). Three subspecies are recognized: the Indian tent turtle, K. t. tentoria (Gray, 1834) in the Mahanadi to Krishna drainages of peninsular India; the plain-bellied tent turtle, K. t. flaviventer (Gunther, 1864) of the northern tributaries of the Ganges from Bihar, India eastward to Bangladesh; and the pink-ringed tent turtle, K. t. circumdata (Mertens, 1969) of the upper and central Ganges river basin in India (Moll, 1987; Das, 1991; Iverson, 1992). Tent turtles are omnivorous, with females being more herbivorous (Moll, 1987). Females are larger than males (Moll, 1987), attaining a maximum size of 27 cm shell length in K. t. circumdata (Das, 1991). This species is found in both small and large rivers. Nesting occurs between October and January depending on the subspecies (Moll, 1987; Das, 1991), and no sexual dichromatism is evident (Moll, 1986). This relatively common species does not currently appear to be threatened (Das, 1991).

Kachuga tecta (Gray, 1831)

The Indian roofed turtle ranges through the Indus to the Narmada and Ganges-Brahmaputra river basins of Pakistan, northern India, probably Nepal, and Bangladesh (Iverson, 1992). No subspecies are currently recognized, although until recently, K. tentoria was commonly considered a subspecies of K. tecta (Moll, 1987). Although reported to be herbivorous (Parshad, 1914), Moll (1987) captured an individual in a hoop trap baited with chicken

entrails. Females are larger than males (Moll, 1987), attaining a maximum shell length of 23 cm (Smith, 1931). This species primarily inhabits lentic habitats (Moll, 1987; Das, 1991) and exhibits no sexual dichromatism (Moll, 1986). The nesting period is unknown, but Moll (1987) noted that a female laid a clutch on January 13. Although this is a common species throughout its range, it is protected under Schedule I of the Indian Wildlife (Protection) Act of 1972, Schedule I of the Bangladesh Wildlife (Preservation) Act of 1974, and Appendix I of CITES (Moll, 1987; Das, 1991).

Kachuga sylhetensis (Jerdon, 1870)

The Assam roofed turtle is found in the Khasi, Garo, and Naga Hill regions of Bangladesh and Assam, India (Moll, 1987). Females are larger than males (Moll, 1987), reaching 19.7 cm shell length (Jerdon, 1870). Nothing is known of the natural history of this species except that it occurs in hill streams (Moll, 1987) and feeds exclusively on freshwater fish in captivity (Das, 1991). This turtle is not protected under the law (Das, 1991).

MATERIALS AND METHODS

The cladistic method (Hennig, 1966; Wiley, 1981) was employed to construct a phylogenetic hypothesis of the batagur complex. In this method, phylogeny is based on shared, derived characters (synapomorphies) instead of overall similarity. Plesiomorphic (primitive) and

apomorphic (derived) character states were determined based on outgroup comparison (Watrous and Wheeler, 1981; Wiley, 1981). Although Hirayama (1984) specified polarity for multistate characters in his cladistic analyses of the Batagurinae, this study follows the recommendation of Swofford (1985), that no a priori character state transformation series be hypothesized (all multistate characters were unordered). Although some debate still exists on this practice (e.g. Mickevich, 1982), it seems that making any a priori assumptions about the polarity of the characters that can not be determined based on outgroup analysis (as is the case with multistate characters) only defeats the purpose of using an outgroup. Finally, the most parsimonious arrangement of taxa was considered to best represent the true phylogeny as evolutionary reversals and parallelism (homoplasy) were minimized (Wiley, 1981; Maddison et al., 1984).

"Character" can be defined as "a feature of an organism which is the product of an ontogenetic or cytogenetic sequence of previously existing features, or a feature of a previously existing parental organism(s)" (Wiley, 1981). The relationship between the terms "character" and "character state" is interpreted to be that defined by Eldridge and Cracraft (1980). In their view, both terms are simply "relative levels of similarity within a given hierarchy." Thus, what is considered a character in an analysis at one taxonomic level (i.e. generic) may be considered a character state in an analysis at an even

higher taxonomic level (i.e. family or order). The PAUP (Phylogenetic Analysis Using Parsimony) computer program version 2.4 (Swofford, 1985) was used to analyze the character state distributions for 60 specimens (Append. A) comprising 12 species. One member of the group, Kachuga sylhetensis, was not examined due to the paucity of skeletal and alcoholic material (only one alcoholic juvenile was available from the British Museum of Natural History). Nevertheless, it is included in the final suggested taxonomy as a member of the Pangshura clade since the general concensus (McDowell, 1964; Moll, 1986) is that it is clearly a member of this species assemblage.

Thirty-five morphological characters of the 12 species (62 specimens total) studied were analyzed (all morphological measurements were taken with vernier callipers). These fall into four broad catagories: cranial osteology (16 characters [following terminology of Gaffney, 1979]), shell morphology (14 characters), epidermal (3 characters), and penial morphology (2 characters) (see append. B for full description). Character states were coded into a discrete data matrix (Table 1), with (0) designating the plesiomorphic and (1) the apomorphic state. Characters exhibiting more than one apomorphic state were coded as 0 = plesiomorphic and 1, 2, or 3 = apomorphic states.

Terminology

Terminology for cranial characters follows Gaffney (1979) whenever possible. However, Gaffney did not

describe the patterns of ridges on the palatal and mandibular triturating surfaces (characters 14 and 15, Append. B). For such cases, terminology was devised to be as clear and descriptive as possible and illustrations were provided when available. In referring to the two generally recognized subgroups within the genus Kachuga, some confusion may result. Herein, these subgroups may appear as "kachuga" or "kachuga group" and "pangshura" or "pangshura" group. Note that in all cases, the name is not capitalized nor is it underlined as would denote any reference to the genus.

The PAUP Program

In the PAUP program, parsimony is indicated by tree length (Swofford, 1985). The most parsimonious tree is the shortest tree, the one which can be constructed in the fewest number of steps (changes from one character state to another).

Only characters with minimal intraspecific variation but which varied between two or more species were selected for analysis. The data matrix was also scanned for the presence of perfectly correlated characters. Perfect correlation could indicate that either the characters are closely linked or that they are not linked but rather represent the same pattern of evolutionary relationship. Any such characters were scrutinized for possible linkage and only those which were considered to be independent due to a clear difference in function or a lack of physical

proximity were included for analysis. PAUP program options used during preliminary analyses were global branch-swapping, mulpars, closest addition sequence, hold set equal to five, and all trees were rooted using Ocadia sinensis as the outgroup based on its apparent close relationship to the ingroup complex. McDowell considered O. sinensis a part of his Batagur complex, while Hirayama (1984) considered it a sister group to a clade consisting of Morenia, Hardella, Kachuga, Batagur, and Callagur. In addition, the penial morphology of Ocadia is similar but not identical to that of the ingroup, exhibiting a triangular plica media but lacking the well-developed flaps found among the ingroup species (Fig. 1).

Global branch-swapping, recommended by Swofford (1985), is a method of "trying out" different arrangements of branches on the cladogram with the goal of finding the arrangement producing the shortest length tree(s). To accomplish this, each branch of the tree is inserted on the developing tree at all possible positions and the consequent length of the resulting tree is calculated.

The mulpars option then stores in memory all of the shortest length trees resulting from one round of branch-swapping for input into the next round of branch-swapping.

The closest addition sequence refers to the order in which the taxa will be added to the tree prior to branch-swapping. In this option, during initial tree construction a taxon is sequentially placed at every possible position on the developing tree; the consequent

length of each possible placement is calculated; and the placement that adds the least length to the tree is chosen. Each of the remaining taxa undergo the same process until all taxa have been added to the tree.

The hold parameter operates during the initial steps of tree construction involving taxa addition. When hold is set equal to n trees and the closest addition sequence is in effect, PAUP will retain the n shortest trees from one step of taxa addition to be used in the next step of taxa addition.

After the phylogeny appeared to be resolved using the mulpars/global branch-swapping "short-cut" method, the data were analyzed again using the branch and bound algorithm which is guaranteed to find all the shortest trees possible based on the data set. In this method, all possible phylogenetic hypotheses are reconstructed and the resultant tree lengths are computed. While much more time-consuming, this method will find any equally parsimonious trees which may have been overlooked using the mulpars/global branch-swapping method.

RESULTS

The characters used in this analysis are described in Appendix B. The data matrix listing the numerical coding for each character as diagnosed for each species is given in Table 1.

Four cladograms were produced (Fig. 2, a-d), each with a length of 59.0 steps and a 0.75 consistency index. The

four topologies result from an unresolved polychotomy which is apparent at node G in the consensus tree (Fig. 3). All other nodes are fully resolved.

The ingroup species arising from node one are well-defined by several completely consistent synapomorphies (Table 2) including large orbito-nasale foramina, the humeral-pectoral sulcus located posterior to the entoplastron, and the fourth marginal scute contacting the first interpleural seam.

Five synapomorphies separate Hardella from Morenia (Table 3) including the presence of a flap-type penis (character 34, Append. B, see also Fig. 1), strongly developed axillary and inguinal buttresses (character 27, Append. B), and a pattern of ridges on the lower jaw (character 14, Append. B, see also Fig. 4) nearly identical to that found in Callagur and K. trivittata (Morenia has a pattern unique among this complex).

Morenia is further distinguished by five autapomorphies (Table 4) including a dorsomedially directed stapedial foramen (character 9, Append. B), inguinal buttresses contacting only the fifth costal plate (character 27, Append. B), and a nontriangular medial fold of the plica media (character 35, Append. B).

While there are two synapomorphies joining the pangshura and the kachuga subgroups of Kachuga (characters 24 and 25, Append. B), a number of characters separate the two groups. Table 5 summarizes the pangshura synapomorphies which include the loss of a medial

premaxillary notch (character 1, Append. B, Fig. 5), the attenuation of the anterior end of the fourth vertebral scute (character 22, Append. B, Fig. 6), and the presence of an eight-sided fourth neural bone (character 23, Append. B, Fig. 7). Further separating the groups is both the location of the apex of the carapace at the level of the second vertebral scute (character 29, Append. B., Fig. 8) in the kachuga, and the persistence of prominent costo-peripheral fontanelles in adult males (character 30, Append. B, Fig. 9).

While Callagur and Batagur share all seven characteristics used by Moll (1986) to diagnose the kachuga subgroup (Table 6), only two of these are considered to be apomorphic states. In this study, Callagur and Batagur are included in the kachuga group clade based on three (cladograms in Fig. 2, a-b) or four characters (cladograms in Fig. 2, c-d). The most consistent of these includes the presence of large costo-peripheral fontanelles in adult males (character 30, Append. B, Fig. 9). These fontanelles are either very small or nonexistent in the pangshura and are absent in Hardella and Morenia. Also very consistent is the extension of the squamosal and/or exoccipital bones to a level well beyond the posterior surface of the occipital condyle (character 12, Append. B). In addition, the apex of the carapace (character 29, Append. B, Fig. 8) is located on the second vertebral scute in the larger Kachugas and Batagur, but is variable in Callagur. Finally, the last character diagnosing this branch in the

cladograms in Figures 2 c-d is the degree of elevation of the coronoid process of the dentary (character 3, Append. B, and Fig. 10). This character, although appearing on this branch, is not very informative since both Batagur and Morenia exhibit the apomorphic state of having a low coronoid process, K. kachuga and K. dhongoka exhibit the alternative apomorphic state of having a high coronoid process, and K. trivittata and Callagur share with Hardella and the pangshuras a moderately elevated coronoid process. Thus, this character serves only to tie Callagur with a single member of the kachuga group.

Other synapomorphies which help to tie Callagur, Batagur, and the large Kachugas together but do not appear as diagnosing the branch include the pattern of ridges on the upper and lower jaws and the presence of seasonal and sexual dichromatism. Regarding the lower jaw (character 14, Append. B, Fig. 4), K. trivittata, Callagur, and Hardella share the apomorphic "Callagur" pattern, while Batagur and K. kachuga share the apomorphic "Batagur" pattern. In respect to the upper jaw (character 15, Append. B, Fig. 11) Batagur and K. kachuga are synapomorphic, having a double alveolar ridge, while K. dhongoka, K. trivittata, Callagur, and the pangshuras possess the plesiomorphic condition of a single denticulated ridge. Hardella and Morenia possess an alternate apomorphic condition (not shown in Fig. 11). Of the constituents of this branch, only K. dhongoka lacks seasonal and sexual dichromatism.

It should be noted that although the relationships between Batagur, Callagur, and the kachuga are not fully resolved and result in four equally parsimonious cladograms, K. dhongoka consistently is the first to diverge from this line and is well diagnosed. The unresolved polychotomy at node G (Fig. 3) consists only of K. kachuga, K. trivittata, Batagur, and Callagur.

DISCUSSION

At node A (Fig. 3), a group of Asian batagurines evolved a suite of unique characteristics distinguishing them from all other members of the family. We have borrowed McDowell's (1964) term "Batagur complex" to designate this group, but the useage is moderately different from that which McDowell envisioned. Herein, the complex excludes Morenia but includes Hardella thurjii, Batagur baska, Callagur borneoensis, Kachuga kachuga, K. trivittata, K. dhongoka, K. smithi, K. tecta, K. tentoria, and K. sylhetensis. Important synapormorphies of this complex are: a flap like penis, large laterally expanded shell buttresses, an extended posterior process of the pterygoid bone, and carapacial striping (later lost in Batagur and K. kachuga).

Based on the ecology of the outgroup taxon Ocadia and the immediate sister group Morenia, the complex probably evolved from ancestors which inhabited lentic habitats such as swamps, lakes, and the backwaters of rivers.

The group then radiated into three major lineages

consisting of a primitive lentic-adapted lineage represented by Hardella, a group of smaller species (the pangshuras) adapted to small streams, rivers, and some lentic situations, and a group of large turtles (the batagurs) adapted to large rivers. Among the latter, K. kachuga, K. trivittata, Callagur, and Batagur have evolved such unusual innovations as seasonal and sexual dichromatism. In the most advanced species of the lineage, Callagur and Batagur, the characteristic elongated fourth vertebral has been reduced to cover only three rather than four or five neurals. However, this is not absolute and occasional Callagur are found in which the fourth vertebral still contacts four neurals. Batagur and Callagur are also atypical in inhabiting brackish water estuaries rather than the up-stream habitats preferred by the kachugas. Kachuga dhongoka, the only member of the large riverine lineage lacking seasonal and sexual dichromatism, appears to be transitional between the batagurs and pangshuras. It resembles the pangshuras by having a simple lower jaw pattern, a similar pattern of articulation of the processus pterygoideus externus with the triturating surface, and a pointed posterior border of the second vertebral (shared with K. tecta and K. tentoria).

Historically, there has been considerable debate about the systematics of this group. The three primary points of contention include: 1.) the relationship between Morenia and Hardella; 2.) the monophyly of the genus Kachuga; and 3.) the position of Batagur and Callagur

relative to the larger members of the Kachuga.

The most recent published research on this group (Hirayama, 1984; Gaffney and Meylan, 1988) visualizes the ingroup as being divided into three sister groups arising from an unresolved trichotomy (node B, Fig. 12). Hardella and Morenia form one sister group, the genus Kachuga forms a second, and Batagur and Callagur form the third. This arrangement is similar to that of McDowell (1964) who placed Hardella, Morenia, and Geoclemys in a Hardella complex, and lumped the Kachugas, Batagur, and Callagur in the Batagur complex with Ocadia, Hieremys, Malayemys, and Chinemys. Geoclemys and the latter three were not considered in this study because more recent authors (Ckhickvadze, 1984; Hirayama, 1984; Carr and Bickham, 1986; Gaffney and Meylan, 1988) consider them as separate lineages from those studied herein. In addition, Hieremys, Malayemys, and Chinemys lack the flap-type penis (character 34, Append. B) (Moll, unpublished). The penis of Geoclemys has not been examined. Ocadia which was used as the outgroup, has the triangular-shaped inner fold of the plica-media (character 35, append. a) which characterizes the flap type penis but lacks prominent flaps on the outer fold of the plica-media (Fig. 1).

The Hardella-Morenia Question

Historically, Hardella has usually been grouped with Morenia (Gray, 1855; Gunther 1864; McDowell, 1964; Hirayama, 1984). McDowell placed them in an "Hardella"

complex along with Geoclemys. Hirayama (1984) and Gaffney and Meylan (1988) depict them as a monophyletic clade on a branch originating from an unresolved trichotomy with the Kachuga and Batagur-Callagur branches. The great similarity in the complex pattern of their palatal ridges implies a close relationship between Hardella and Morenia. However, Hardella's synapomorphies with the Kachuga-Batagur-Callagur line (e.g. expanded buttresses and flap-type penis) indicate a closer relationship to the river turtles. These results suggest that the clade proposed by Hirayama (1984) and Gaffney and Meylan (1988) is polyphyletic.

The Kachuga-Pangshura Question

MacDowell suggested that the great disparity in the characteristics of K. trivittata and K. tecta, representing the extremes of the Kachuga continuum, warranted generic separation (Table 7). However, the similarity of the more intermediate K. dhongoka and K. smithi "partially bridge this gap."

Over a century earlier, Gray (1855) had recognized these as two distinct species groupings with sufficient differences to warrant the subgeneric divisions Kachuga and Pangshura of the genus Batagur. As an aside, some confusion has resulted from this publication, since Gray's drawing of the skull and jaw labeled K. dhongoka was actually a K. kachuga, an error which has been perpetuated in Wermuth and Mertens, 1961, page 119, abb. 86 and in

Gaffney, 1979, pages 325-326, figs. 240 and 241.

In later studies, Gunther (1864) and Gray (1869), elevated these subgenera to generic rank (Kachuga and Pangshura). However, Boulenger (1889) returned both to a single genus (i.e. Kachuga). In 1986, Moll resurrected the subgenera based on the suites of characters presented in Table 6.

The results of this study indicate that Kachuga, as presently classified, is paraphyletic in that Callagur and Batagur have been excluded from the genus (Fig. 3).

The Batagur-Callagur-Kachuga Question

The monophyly of Callagur and Batagur with the larger Kachugas and the divergence of the smaller Kachugas from this clade as shown in these results is not unexpected, since it has been suggested by earlier researchers. McDowell (1964) recognized a very close relationship between two of the larger riverine Kachugas (K. kachuga and K. trivittata) and Callagur, especially between K. trivittata and Callagur.

"It is with the gravest misgivings that I keep Callagur separate from Kachuga. The single species, C. borneoensis, is closely related to Kachuga trivittata and is geographically representative of that species...I suspect that Callagur borneoensis, Kachuga trivittata, and K. kachuga will turn out to be a single superspecies."

McDowell also mentions the similarity between Kachuga, Callagur, and Batagur in skull morphology, but noted that Batagur differed by having a four clawed manus and an extra denticulated ridge in the upper jaw. Findings from this study indicate only the former trait is unique as the double palatal ridge is shared with K. kachuga. McDowell did not indicate whether Batagur was more closely aligned with Callagur or Kachuga.

The relationships proposed by McDowell are supported in my cladogram. Callagur and Batagur appear on the same branch as the larger Kachugas, while the pangshura form a sister group to the Batagur-Callagur-Kachuga lineage. This differs from Hirayama's scheme in which Batagur and Callagur form a sister group to the monophyletic genus Kachuga, which arises from an unresolved trichotomy (Fig. 12, node B).

In this study, K. dhongoka diverges first in the Batagur-Callagur-Kachuga line (Fig. 3, node F), suggesting a more intermediate relationship with the pangshura line in which K. smithi diverges first. This pattern is reminiscent of that proposed by McDowell (1964). Supporting the intermediate role of K. dhongoka is its lack of seasonal and sexual dichromatism shared by the other members of the Batagur-Callagur-Kachuga assemblage. In addition, K. dhongoka possesses a simple lower jaw pattern identical to that of the pangshuras (character 14, Append. B, see also Fig. 4). Finally, the single apomorphy resulting in the divergence of dhongoka from the its

ancestral node with the Batagur-Callagur-Kachuga line is an homoplasy shared with K. tecta.

The differences between the findings of this study and that of MacDowell (1964) might be attributed to the fact that: 1.) he was not able to examine as many members of the Kachuga (he did not examine K. kachuga and K. dhongoka); 2.) he relied primarily on skull characters; and 3.) his approach was not a cladistic one.

Although Hirayama (1984) did use the cladistic approach, he did not examine K. kachuga and K. dhongoka. Further, it appears that he ordered his multistate characters which I did not.

Further study of the systematics of this group is definitely warranted to confirm the findings delineated herein and to resolve the relationships within the Batagur-Callagur-kachuga group line. The use of molecular cladistics would be especially beneficial.

Taxonomic Revision

This study is the most complete examination of this complex to date, including all but one species of Kachuga. The results suggest that some taxonomic revision is warranted (Table 8). Based on the phylogenetic hypothesis obtained herein, Morenia and Hardella should retain generic rank based on Wiley's Convention 2 (1981, p. 205) which states: "...natural taxa of essential importance to the group classified will be retained at their traditional

ranks whenever possible, consistent with phylogentic relationships and the taxonomy of the group as a whole."

Based on the phylogeny presented herein, previous classifications of the remaining taxa are paraphyletic, excluding Batagur and Callagur from the kachuga group. Two arrangements are possible for the remaining ingroup taxa. In the first, all are synonymized under Batagur (Gray, 1855), forming one large genus arising from node A (Fig. 13). This would contain two subgenera: Batagur (comprised of Kachuga dhongoka, K. kachuga, K. trivittata, Callagur borneoensis, and Batagur baska), and Pangshura (comprised of K. smithi, K. tecta, K. tentoria, and K. sylhetensis). An alternate arrangement would include B. baska and C. borneoensis with the kachuga group as the genus Batagur while elevating the pangshura group to generic rank, with two subgenera in each (Fig. 14). The latter arrangement seems more informative since the pangshura are better defined than Hardella. If the latter is to be given generic rank, the former should be as well.

Pangshura rather than Kachuga must be used as the name for this group. Depending on the source (Wermuth and Mertens, 1977 or Smith, 1931), either Kachuga kachuga or K. trivittata is the type species for the genus Kachuga*. As both are members of the newly formed Batagur, the name Kachuga is unavailable for the pangshura group generic name. Instead, Kachuga tentoria = Pangshura flaviventer (Gunther, 1864) is the type species for the genus, making Pangshura the available name for this group.

Within the genus Batagur, the subgenus Batagur (Gray, 1855) is comprised of B. trivittata, B. kachuga, B. borneoensis, and B. baska. The remaining member of the genus, B. dhongoka, forms the monotypic subgenus Dongoka (Gray, 1869 through monotypy and tautonomy).

Within the Pangshura, P. tecta and P. tentoria form the subgenus Pangshura. Pangshura smithi forms a monotypic subgenus Emia (after Emia smithi, type species through monotypy of Gray, 1870). Pangshura sylhetensis superficially appears to belong in the more advanced subgenus Pangshura, but it was excluded from the study and its position is uncertain.

* NOTE:

Wermuth and Mertens (1977) and King and Burke (1989) consider K. kachuga as Gray's (1831 "1830-35") Emys kachuga to be the type species for the genus by absolute tautonomy. However, Iverson (1992) follows Smith (1931) who designated K. trivittata as type species for the genus.

Diagnosis of Genera

Morenia Gray, 1870

Type species: Lindholm (1929): Emys berdmorei (Blyth, 1858) = Morenia ocellata (Dumeril and Bibron, 1835).

Diagnosis: Upper jaw characterized by a medial premaxillary notch; frontal bone precluded from the orbit rim by the juncture of the anterior edge of the parietal bone and the posterior edge of the prefrontal bone; processus pterygoideus externus articulates with the

tritulating surface at the same level, with surface roughened (a trait shared with Hardella); posteroventral process of the jugal bone shorter than the posteroventral process of the maxilla; posterior process of the pterygoid does not extend posterior to the basisphenoid; stapedia foramen directed dorsomedially; lower jaw characterized by the presence of a midsagittal ridge and an alveolar ridge which is located midway between the anterior and posterior margins of the jaw; upper jaw characterized by the presence of a single alveolar ridge, double anterior parasagittal ridges, and a single posterior midsagittal ridge (very similar to the upper jaw of Hardella); anterior edge of the fourth vertebral scute broad; fourth neural bone six-sided; axillary and inguinal buttresses weakly developed; superior edge of the inguinal buttress contacts only the fifth costal plate; apex of the carapace located at the level of the third vertebral scute; costo-peripheral fontanelles absent in adults; seasonal and sexual dichromatism lacking; carapace unstriped (a trait shared with Batagur baska and B. kachuga); penis lacks distinctively pointed distal flaps on lateral folds of the plica media; medial fold of the plica media not triangular in shape.

Two species: M. petersi and M. ocellata

Hardella Gray, 1870

Type species: Emys thurjii Gray (1870) by monotypy.

Diagnosis: Upper jaw characterized by a medial premaxillary notch; frontal bone participates in the

formation of the edge of the orbit rim; processus pterygoideus externus has roughened surface and articulates with the triturating surface at same level, as in Morenia; posteroventral process of the jugal even with or posterior to the posteroventral process of the maxilla; posterior process of the pterygoid does not extend beyond the basisphenoid; stapedia foramen directed posteriorly; anterior extension of the frontal bones shorter than half the length of the prefrontals; lower jaw characterized by the presence of double anterior parasagittal ridges, an alveolar ridge located at the posterior margin of the jaw, and the absence of posterior midsagittal or parasagittal ridge(s) (similar to the condition in Batagur borneoensis and B. trivittata); upper jaw characterized by the presence of a single alveolar ridge, double anterior parasagittal ridges and a single posterior midsagittal ridge (similar to the condition in Morenia); anterior edge of the fourth vertebral broad; fourth neural six-sided; axillary and inguinal buttresses well developed; inguinal buttress contacts the sixth costal plate; apex of the carapace located at the level of the third vertebral scute as in Morenia, Pangshura, and sometimes Batagur borneoensis; large costo-peripheral fontanelles absent in adults; seasonal and sexual dichromatism lacking (a trait shared with Morenia, Pangshura, and Batagur dhongoka); three carapacial stripes present in juveniles and males; penis characterized by lateral folds of the plica media with

distinctively pointed flaps; medial fold of the plica media triangular in shape.

A single species: Hardella thurjii

Batagur Gray, 1855

Type species: Emys batagur (Gray, 1831 "1830-35")
= Batagur baska (Gray, 1855) through tautonomy.

Diagnosis: Upper jaw characterized by a medial premaxillary notch; frontal bone participates in the formation of the edge of the orbit rim; articulating surface of the processus pterygoideus externus superior to that of the triturating surface in all except B. dhongoka, which resembles Pangshura by having the processus pterygoideus externus articulate at the same level; posteroventral process of the jugal even with or posterior to the posteroventral process of the maxilla; posterior process of the pterygoid does not extend posterior to the basisphenoid; the stapedia foramen directed posteriorly; form of the upper and lower jaws interspecifically variable; anterior end of the fourth vertebral broad; fourth neural six-sided; axillary and inguinal buttresses well developed; inguinal buttresses contact the sixth costal plate; apex of the carapace located at the level of the second vertebral (often at the third vertebral in B. borneoensis); large costo-peripheral fontanelles present in adult males; pronounced seasonal and sexual dichromatism displayed in all except B. dhongoka; carapaces_of B. dhongoka, B. trivittata, and B. borneoensis exhibit

three stripes but B. baska and B. kachuga are not patterned; penis is characterized by pointed flaps on lateral folds of plica media; medial fold of plica media triangular.

Five species: Batagur baska, B. borneoensis, B. dhongoka, B. kachuga, and B. trivittata.

Pangshura Gunther, 1864

Type species: Emys tecta (Gray, 1831)

Diagnosis: Upper jaw unnotched; frontal bone participates in the formation of the edge of the orbit rim; processus pterygoideus externus articulates with the triturating surface at the same level and has a relatively smooth surface; posteroventral process of the jugal even with or posterior to the posteroventral process of the maxilla; posterior process of the pterygoid does not extend posterior to the basisphenoid; stapedia foramen directed posteriorly; anterior extension of the frontal bones longer than half the length of the prefrontal bones; lower jaw characterized by the presence of a single midsagittal anterior ridge, an alveolar ridge located along the posterior margin of the jaw, and the absence of posterior midsagittal and parasagittal ridge(s); upper jaw resembles that of B. borneoensis, B. dhongoka, and B. trivittata in possessing a single alveolar ridge and lacking separate anterior midsagittal and parasagittal ridges; anterior edge of the fourth vertebral scute narrows anteriorly to a point; fourth neural bone eight-sided; axillary and

inguinal buttresses well developed; inguinal buttresses contact the sixth costal plate; apex of the carapace at the level of the third vertebral scute; large costo-peripheral fontanelles absent in adults; seasonal and sexual dichromatism lacking; carapace marked by a single median stripe; penis characterized by lateral folds of the plica media possessing distinctively pointed flaps; medial fold of the plical media triangular in shape.

Four species: Pangshura smithi, P. tecta, P. tentoria, and P. sylhetensis.

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Table 1. Numerical matrix for data set. 0 denotes the plesiomorphic state, 1, 2, or 3 denotes the apomorphic states.

Species	Character state
<u>Q. sinensis</u>	000000000000000000000000000000000000
<u>K. dhongoka</u>	00200011001100011100100122001100210
<u>K. kachuga</u>	00210011001102211100000122001101010
<u>K. trivittata</u>	00010011001111011100000122001101210
<u>K. smithi</u>	10000011001010011110011122000000110
<u>K. tecta</u>	10000111001010011101111122010000110
<u>K. tentoria</u>	10000011001010011111011122010000110
<u>B. baska</u>	00110011001112211100000212001111010
<u>C. borneoensis</u>	00010011001111011100000212000101210
<u>H. thurjii</u>	00020011001001111100000212000000210
<u>M. petersi</u>	01121010111013111100000211100000001
<u>M. ocellata</u>	011210101010?3111100000211100000001

Table 2. Synapomorphies diagnosing the ingroup species--
Batagur baska, Callagur borneoensis, Hardella thurjii,
Kachuga trivittata, K. kachuga, K. dhongoka, K. smithi,
K. tecta, K. tentoria, Morenia petersi, and M.
ocellata.

Character	Ocadia	Ingroup Species
superior temporal emargination	not anterior to quadrate	anterior to quadrate
orbito-nasale foramen	small	large
maxilla	not serrated	serrated
humero-pectoral sulcus	crosses entoplastron	does not cross entoplastron
1st interpleural seam	does not contact 4th marginal	does contact 4th marginal

Table 3. Synapomorphies separating Hardella and members of the ingroup from Morenia.

Character	#	<u>Hardella</u> , etc.	<u>Morenia</u>
Penis*	34	flap type	lacking flaps
Plastral buttresses*	27	well developed	weakly developed
Lower jaw	14	<u>Callagur</u> type	<u>Morenia</u> type
Pterygoid*	8	extends posterior to basisphenoid	not posterior to basisphenoid
Carapacial stripes	33	three	none

* synapomorphic with all members of the ingroup except Morenia.

Table 4. Autapomorphies of Morenia.

Character	#	<u>Morenia</u>	Other Ingroups
Orbit rim	2	frontal bone precluded	frontal bone incorporated
Posteroventral process of jugal	5	reduced	well developed
Stapedial foramen	9	directed dorsomedially	directed posteriorly
Inguinal buttress	27	contacts only costal plate 5	contacts costal plate 6
Medial fold of plica media	35	not triangular	triangular

Table 5. Synapomorphies separating the pangshura group from the kachuga group.

Character	pangshura	kachuga
Upper jaw	unnotched	medial notch
Posterior edge of palatine	elongated	not elongated
Frontal bones	elongated	not elongated
2nd vertebral seam	on 2nd neural ¹	on third neural
4th vertebral	narrows anteriorly	does not narrow anteriorly
4th neural	eight-sided	six-sided
Carapace	one stripe	three striped or unmarked

1 - a reversal occurs in that in *K. tecta* the second vertebral seam is located on the third neural

Table 6. Diagnostic characters of the kachuga and pangshura subgroups. (After Moll, 1986 - table 1, p. 542)

Character	kachuga	pangshura
Upper jaw	medial notch weakly bicuspid	unnotched
Neural formula	4,6>6>6>6>6>6>4-6>	4,6>6>8,4,6>6>4-6>
Apex of shell	vertebral 2	vertebral 3
4th vertebral scute	broad anteriorly overlaps 4 neurals	narrow anteriorly overlaps 5 neurals
Costo-peripheral fontanelles	remain prominent in males	fused by maturity or very small
Carapace	three striped or unmarked	usually median stripe only
Maximum size	>40 cm CL	<30 cm CL

Table 7. Differences between K. trivittata and K. tecta as noted by McDowell (1964).

Character	<u>K. trivittata</u>	<u>K. tecta</u>
adult size	large	small
anterior neurals	elongated	short
phalanges on 5th toe	four	three
4th vertebral scute	rectangular	narrows anteriorly
tomium	medially notched	not medially notched
dorsal ridge	obscure	well defined

Table 8. Proposed Taxonomic Revisions

Family Bataguridae

Subfamily Batagurinae

Genus Batagur

Subgenus Batagur

B. baska

B. borneoensis (formerly Callagur borneoensis)

B. kachuga (formerly Kachuga kachuga)

B. trivittata (formerly Kachuga trivittata)

Subgenus Dongoka

B. dhongoka (formerly Kachuga dhongoka)

Genus Pangshura

Subgenus Emia

P. smithi (formerly Kachuga smithi)

Subgenus Pangshura

P. tecta (formerly Kachuga tecta)

P. tentoria (formerly Kachuga tentoria)

P. sylhetensis (formerly Kachuga sylhetensis)

Genus Hardella

Hardella thurjji

Genus Morenia

M. petersi

M. ocellata

Appendix A. Specimens examined.

Abbreviations are: AMNH = American Museum of Natural History; BMNH = British Museum of Natural History; EOM = personal collection of Dr. Edward O. Moll; FMNH = Field Museum of Natural History; PCHP = personal collection of Dr. Peter C. H. Pritchard; UF = University of Florida.

Species	Catalogue #	Description
<u>Ocadia sinensis</u>	AMNH 30173	alcoholic
	AMNH 30176	alcoholic
	AMNH 30183	alcoholic
	AMNH 30186	alcoholic
	AMNH 30191	alcoholic
	AMNH 30192	skeleton
	AMNH 30196	skull
	* PCHP	skull/disart. skeleton
	PCHP 1086	shell
	PCHP 1085	alcoholic
	PCHP 1984	alcoholic
	UF 57412	
	UF 61965	
UF 62054		
UF 63385		
<u>Morenia petersi</u>	EOM 2884/FMNH 224146	alcoholic
	EOM 2885/FMNH 224150	skeleton
	EOM 2999	skeleton & penis
	EOM 3000	skeleton & penis
<u>Morenia ocellata</u>	BMNH 87.3.11.7	skeleton (no skull)
	BMNH 87.3.11.6	skeleton
	BMNH 91.11.26.2	alcoholic
<u>Hardella thurjii</u>	EOM 2806/FMNH 224135	alcoholic
	EOM 2654/FMNH 224153	skull/shell
	* EOM	
<u>Callagur borneoensis</u>	EOM 2324/FMNH 224107	skeleton (no shell)
	EOM 2339/FMNH 224102	skeleton (no shell)
	EOM 2220/FMNH 224098	skeleton (no shell)
	* EOM	shell
	EOM 2462	alcoholic

Appendix A - cont'd.

<u>Batagur</u> <u>baska</u>	EOM 2286/FMNH 224097	skull
	EOM 2287/FMNH 224124	skull
	* EOM	alcoholic
	* EOM	alcoholic
<u>Kachuga</u> <u>kachuga</u>	EOM 2794/FMNH 224152	skeleton
	EOM 2802	shell,
		alcoholic
		head & legs
	EOM 2578	shell
<u>Kachuga</u> <u>dhongoka</u>	EOM 2776/FMNH 224154	skeleton
	EOM 2574	shell
	EOM 2577	shell
	* EOM	alcoholic
	EOM 2813	alcoholic
<u>Kachuga</u> <u>trivittata</u>	BMNH 1947.3.4.86	skull:
	(formerly 68.5.11.10)	holotype of
		<u>K. peguensis</u>
	BMNH 1947.3.4.85	skull:
	(formerly 67.9.28.4)	holotype of
		<u>Kachuga</u>
		<u>trilineata</u>
	AMNH 58560	shell/skull
	AMNH 58565	shell/skull/
		partial
		skeleton
<u>Kachuga</u> <u>tentoria</u>	EOM 2674/FMNH 224141	alcoholic
	EOM 2576/FMNH 224105	shell/partial
		skeleton
	EOM 2651/FMNH 224185	skeleton
	EOM 3028	skeleton
	* EOM	alcoholic
	* EOM	alcoholic
	EOM 2670	alcoholic
	EOM 2632	alcoholic
	EOM 2771	alcoholic
	EOM 2955	alcoholic
<u>Kachuga</u> <u>tecta</u>	EOM 2653	skeleton
<u>Kachuga</u> <u>smithi</u>	* EOM	alcoholic
	EOM 2955	alcoholic
	EOM 2771/FMNH 224132	alcoholic
	EOM 2652/FMNH 224186	skeleton
	EOM 3033	skeleton

* no catalog number available

Appendix B. Character Descriptions

For each character, the variation within the Batagur complex is discussed, polarity based on outgroup analysis is noted, and a description of character states and the numerical coding for each is given.

Cranial Osteology

1. Presence of medial premaxillary notch (Hirayama, 1984; Moll, 1986)

Variation - The absence of a medial premaxillary notch in the pangshura subgroup of the Kachuga has consistently been used to separate it from the kachuga subgroup (McDowell, 1964; Moll, 1986). This notch is present in all other members of the ingroup species (Fig. 5).

Polarity - In the outgroup, a medial premaxillary notch is present. This state is considered plesiomorphic.

States - 0 = medial premaxillary notch present

1 = medial premaxillary notch absent

2. Frontal exposure onto edge of orbit rim

Variation - In most members of the ingroup species, the frontal bones form part of the edge of the orbit rim. It is only in the genus Morenia that the frontal bone is precluded from the orbit rim by the juncture of the anterior edge of the parietal bone and the posterior edge of the nasal bone.

Polarity - In the outgroup, the frontal bone participates in the formation of the edge of the orbit rim. This state is considered plesiomorphic.

States - 0 = the frontal bone participates in the formation of the edge of the orbit rim.

1 = the frontal bone does not participate in the formation of the edge of the orbit rim.

3. Elevation of the coronoid process of dentary

Variation - The degree of elevation of the coronoid process within the study taxa is classified as high, moderate, or low. This character was described as the height (measured with vernier calipers) of the coronoid as a percentage of the length of the dentary, and the three classifications reflect natural breaks in the data. Within the ingroup species, only Morenia and Batagur possess low coronoid processes. Similarly, only K. dhongoka and K. kachuga exhibit highly elevated coronoids, while K. trivittata, Callagur, Hardella, and all members of the pangshura have moderate elevation (Fig. 10).

Polarity - In the outgroup, the coronoid process is moderately elevated. This state is considered plesiomorphic.

States - 0 = moderately (height of coronoid is 28% - 33% of length of dentary)

1 = high (height of coronoid is 35% - 41% of length of dentary)

2 = low (height of coronoid is 20% - 25% of length of dentary)

4. Articulation of processus pterygoideus externus with

tritulating surface

Variation - The processus pterygoideus externus articulates with the tritulating surface in one of three ways: a.) at the same level with a relatively smooth surface as is found in K. dhongoka and the pangshura; b.) at the same level but the surface is roughened as is found in Hardella and Morenia; or c.) articulating surface superior to that of the tritulating surface as found in K. kachuga, K. trivittata, Batagur, and Callagur.

Polarity - In the outgroup, the articulation of the processus pterygoideus externus with the tritulating surface is at the same level and not roughened. This state is considered plesiomorphic.

States - 0 = same level, smooth

1 = different level

2 = same level, roughened

5. Development of posteroventral process of jugal

Variation - The degree of development of the posteroventral process (p.p.) of the jugal is defined based on a comparison with the p.p. of the maxilla. Only Morenia exhibits a reduced p.p. of the jugal in which the process is directed posteriorly but is shorter than the p.p. of the maxilla. The remaining ingroup species possess a well-developed p.p. of the jugal which is both posteriorly directed and longer than the p.p. of the maxilla.

Polarity - In the outgroup, the posteroventral process of the jugal is posteriorly directed and longer than the

posteroventral process of the maxilla. This state is considered plesiomorphic.

States - 0 = well developed--as long or longer than posteroventral process of maxilla

1 = reduced--posteriorly directed but shorter than posteroventral process of maxilla

6. Posteroventral process of maxilla contact with processus pterygoideus externus

Variation - Only in K. tecta is contact between the posteroventral process of the maxilla and the processus pterygoideus externus prevented by a lateral extension of the palatine. In all other ingroup species, these two processes articulate.

Polarity - In the outgroup, the posteroventral process of the maxilla contacts the pterygoideus externus. This state is considered plesiomorphic.

States - 0 = yes

1 = no--contact prevented by lateral extension of palatine

7. Position of the anterior margin of superior temporal emargination in relation to the tympanic fossa.

Variation - In all ingroup species, the anterior margin of the superior temporal emargination is located anterior to the tympanic fossa.

Polarity - In the outgroup, the anterior margin of the superior temporal emargination is even with the anterior edge of the tympanic fossa. This state is considered

plesiomorphic.

States - 0 = located even with the tympanic fossa
1 = located anterior to the tympanic fossa

8. Posterior process of pterygoid relative to the basisphenoid

Variation - The posterior process of the pterygoid extends posterior to the basisphenoid in all members of the ingroup species except Morenia.

Polarity - In the outgroup species, the posterior process of the pterygoid extends posterior to the basisphenoid. This state is considered plesiomorphic.

States - 0 = extends posterior to the basisphenoid
1 = does not extend posterior to the basisphenoid

9. Direction of exit for the stapedia foramen

Variation - Only in Morenia is the stapedia foramen directed dorsomedially. In all other ingroup species, the stapedia foramen is directed posteriorly.

Polarity - In the outgroup species, the stapedia foramen is directed posteriorly. This state is considered plesiomorphic.

States - 0 = directed posteriorly
1 = directed dorsomedially

10. Postorbital contact with maxilla

Variation - Only in M. petersi does the postorbital contact the maxilla. In all other ingroup species (including M. ocellata), contact is prevented by the jugal.

Polarity - In the outgroup species, the postorbital does not contact the maxilla. This state is considered plesiomorphic.

States - 0 = postorbital does not contact maxilla

1 = postorbital contacts maxilla

11. Size of the orbito-nasale foramina

Variation - All ingroup species possess orbito-nasale foramina are distinctively larger than those found in Ocadia sinensis.

Polarity - In the outgroup species, the orbito-nasale foramina are small. This state is considered plesiomorphic.

States - 0 = small

1 = large

12. Posterior edge of the squamosal and/or exoccipital bone(s) relative to the posterior surface of the occipital condyle

Variation - In Batagur, Callagur, and all members of the kachuga group, the squamosal and/or exoccipital bone(s) projects posteriorly well beyond the occipital condyle. In Hardella, Morenia, and all members of the pangshura group, the squamosal and/or exoccipital bone(s) are approximately even with or anterior to the occipital condyle.

Polarity - In the outgroup species, the squamosal and/or exoccipital bone(s) does not project beyond the occipital condyle. This state is considered plesiomorphic.

States - 0 = even with the occipital condyle
1 = posterior to the occipital condyle

13. Anterior extension of frontal bones relative to the length of the prefrontal bones

Variation - In Hardella, M. ocellata, and two of the kachuga group (K. kachuga and K. dhongoka), the anterior extension of the frontal bones is shorter than half the length of the prefrontal bones. However, in M. petersi, Callagur, Batagur, all members of the pangshura group, and the remaining member of the kachuga group (K. trivittata), the extension of the frontal bones exceeds half the length of the prefrontal bones.

Polarity -In the outgroup species, the length of the anterior extension of the frontal bones is shorter than half the length of the nasal bones. This state is considered plesiomorphic.

States - 0 = shorter than half the length of prefrontal bones
1 = longer than half the length of prefrontal bones

14. Ridge pattern of the lower jaw

Variation - Four basic patterns of ridges are found on the lower jaw:

Ocadia type:

K. dhongoka and all members of the pangshura group exhibit a type of lower jaw pattern in which the alveolar ridge is located at the posterior margin of the

jaw or nearly so, a single midsagittal anterior ridge is present, and no posterior midsagittal or parasagittal ridge(s) is present (Fig. 4, D and E).

Callagur type:

In Callagur, K. trivittata, and Hardella the alveolar ridge is located at the posterior margin of the jaw or nearly so, double anterior parasagittal ridges are present, and posterior midsagittal or parasagittal ridge(s) are absent (Fig. 4, C and F).

Batagur type:

Batagur and K. kachuqa exhibit the Batagur type lower jaw structure in which the primary alveolar ridge is located midway between the anterior and posterior margins of the jaw, and a single anterior midsagittal ridge and a pair of posterior parasagittal ridges are present (Fig. 4, A and B).

Morenia type:

M. petersi and M. ocellata exhibit a lower jaw structure in which the alveolar ridge is located midway between the anterior and posterior margins of the jaw, and a single anterior midsagittal ridge and posterior midsagittal ridge are present.

Polarity - In the outgroup species, the lower jaw is of the Ocadia type. This state is considered plesiomorphic.

- States - 0 = Ocadia type
1 = Callagur type
2 = Batagur type
3 = Morenia type

15. Ridge pattern of the upper jaw

Variation - Three basic patterns of ridges are found on the upper jaw:

Ocadia type:

Callagur, the pangshura group, and two members of the kachuga group (K. dhongoka and K. trivittata) display an Ocadia type upper jaw structure in which a single alveolar ridge is present, separate anterior midsagittal or parasagittal ridge(s) are lacking although the medial ends of the alveolar ridge may curve forward, and a posterior midsagittal ridge may or may not be present (Fig. 11A).

Morenia type:

Hardella and Morenia exhibit a type of upper jaw structure in which a single alveolar ridge, double anterior parasagittal ridges, and a single posterior midsagittal ridge are present.

Batagur type:

In Batagur and K. kachuga the upper jaw structure which comprises a double alveolar ridge, double anterior parasagittal ridges, and a single posterior midsagittal ridge are present (Fig. 11b).

Polarity - In the outgroup, the form of the upper jaw

is of the Ocadia type. This state is considered plesiomorphic.

- States - 0 = Ocadia type
- 1 = Morenia type
- 2 = Batagur type

16. Serrate maxilla

Variation - All members of the ingroup species have serrated maxilla.

Polarity - In the outgroup, the maxilla lack serrations. This state is considered plesiomorphic.

- States - 0 = not serrate
- 1 = serrate

Shell Morphology

17. Position of the humeral-pectoral sulcus in relation to the entoplastron

Variation - In all members of the ingroup species, the humeral-pectoral sulcus is located anterior to the entoplastron.

Polarity - In the outgroup species, the humeral-pectoral sulcus crosses the entoplastron. This state is considered plesiomorphic.

- States - 0 = crosses the entoplastron
- 1 = anterior to the entoplastron

18. Marginal contact of the first interpleural seam

Variation - In all members of the ingroup species, the seam between the first and second pleural scutes contacts

the fourth marginal scute.

Polarity - In the outgroup species, the first interpleural seam contacts the fifth marginal scute. This state is considered plesiomorphic.

States - 0 = seam is posterior to marginal #4

1 = seam contacts marginal #4

19. Neural contact of second intervertebral seam

Variation - In two members of the pangshura group (K. smithi and K. tentoria), the second vertebral seam crosses or traverses the second neural bone. In the remaining ingroup species, it crosses the third neural.

Polarity - In the outgroup species, the second vertebral seam is located on the third neural bone. This state is considered plesiomorphic.

States - 0 = crosses third neural

1 = crosses second neural

20. Shape of the posterior edge of third vertebral scute

Variation - The posterior edge of the third vertebral scute is pointed posteriorly in two members of the pangshura group (K. tecta and K. tentoria) while in all other ingroup species the edge is straight.

Polarity - In the outgroup species, the posterior edge of the third vertebral scute is straight. This state is considered plesiomorphic.

States - 0 = straight

1 = pointed posteriorly

21. Shape of the posterior edge of second vertebral scute

Variation - Only in K. tecta and K. dhongoka is the posterior edge of the second vertebral scute pointed posteriorly. In all other ingroup species, the edge is straight.

Polarity - In the outgroup species, the posterior edge of the second vertebral scute is straight. This state is considered plesiomorphic.

States - 0 = straight

1 = pointed posteriorly

22. Shape of the anterior edge of fourth vertebral scute

Variation - This character has been used consistently (Smith, 1931; McDowell, 1964; Moll, 1985) to separate the currently designated pangshura group from the kachuga group. In the pangshura, the anterior edge of the fourth vertebral scute is attenuated to form a point. In all other members of the ingroup species, the anterior edge of the fourth vertebral broadly contacts the third vertebral (Fig. 6).

Polarity - In the outgroup species, the anterior edge of the fourth vertebral scute is straight. This state is considered plesiomorphic.

States - 0 = straight

1 = pointed anteriorly

23. Number of sides on the fourth neural bone

Variation - In the pangshura, the fourth neural bone is typically eight-sided, but in the remaining members of

the ingroup species, it is six-sided (Fig. 7).

Polarity - In the outgroup species, the fourth neural is six-sided. This state is considered plesiomorphic.

States - 0 = 6-sided

1 = 8-sided

24. Neural bones covered by fourth vertebral scute

Variation - In Batagur, Callagur, Hardella, and Morenia, the fourth vertebral scute is only slightly longer than it is wide and overlies three neural bones. However, in all members of the Kachuga, the fourth vertebral scute is substantially longer than it is wide and overlies four to five neural bones.

Polarity - In the outgroup species, the fourth vertebral scute is only slightly longer than it is wide, as in Batagur, Callagur, Hardella, and Morenia, but it overlies four neurals instead of three. This state is considered plesiomorphic.

States - 0 = not substantially longer than wide,
covering four neurals

1 = substantially longer than wide, covering
four to five neurals

2 = not substantially longer than wide,
covering three neurals

25. Costal bones contacted by fourth vertebral scute

Variation - In Hardella, Morenia, Callagur, and Batagur, the fourth vertebral scute overlies the fifth, sixth, and seventh costal plates. In all members of the

Kachuga, however, the fourth vertebral scute extends anteriorly to reach the fourth costal plate (see note below) and posteriorly to the seventh or sometimes the eighth costal plate.

Polarity - In the outgroup species, the fourth vertebral scute overlies the fifth, sixth, seventh, and eighth costal plates. This state is considered plesiomorphic.

States - 0 = overlies costals 5-6-7-8

1 = overlies costals 5-6-7

2 = overlies costals 4-5-6-7-(sometimes 8)

NOTE: Although in the pangshura group, the fourth vertebral overlies costals 5-6-7-(sometimes 8), I have included it in this category with the kachuga group (which have the fourth vertebral overlying costals 4-5-6-7) because the restriction of the anterior margin of the fourth vertebral in the pangshura group prevents this scute from contacting the fourth costal, even though it is located anteriorly enough to do so otherwise. This seems to be a valid treatment of the character because this is actually a description of the position of the entire fourth vertebral scute in relation to the costal bones, rather than just seam/costal plate contact.

26. Development of axillary and inguinal buttresses

Variation - The development of the axillary and inguinal buttresses can be described as moderate, short (as in Morenia), or well developed (as in the remaining ingroup

species). In the short state, the medial edges of the axillary and inguinal buttresses project only slightly into the central space of the shell. However, in the well-developed state, the buttresses are much thicker and well developed, the medial edges being located much further into the central space of shell.

Polarity - In the outgroup species, the axillary and inguinal buttresses are moderately developed, more than in Morenia, but less than in the well-developed state. This state is considered plesiomorphic.

States - 0 = moderate

1 = short

2 = well developed

27. Inguinal buttress contact with costal plates

Variation - Among the species examined, the superior edge of the inguinal buttress contacted the carapace in one of two positions, as first described by Boulenger (1890). In Morenia, contact was with the fifth costal plate. In all other ingroup species, the buttress contacted the sixth costal plate, either being achylosed between the fifth and sixth plates or by contacting the extreme anterior edge of the sixth plate alone.

Polarity - In the outgroup species, the inguinal buttress contacts the sixth costal plate. This state is considered plesiomorphic.

States - 0 = contacts costal plate #6

1 = contacts costal plate #5 only

28. Shape of the carapace

Variation - The carapace is distinctively high vaulted in only two members of the pangshura group included in this study (K. tecta and K. tentoria) (see note below). In all other ingroup species, the carapace is only moderately vaulted.

Polarity - In the outgroup species, the carapace is only moderately vaulted. This state is considered plesiomorphic.

States - 0 = moderately vaulted

1 = high vaulted

Note: K. sylhetensis, generally included in of the pangshura group (Moll, 1987) has a high vaulted shell.

29. Location of the highest point (apex) of the carapace

Variation - In Batagur and the kachuga group, the apex of the carapace is located at the level of the second vertebral scute. In the pangshura group, Hardella, and Morenia, the apex is at the level of the third vertebral scute. The location is variable in Callagur and therefore is coded as a question mark.

Polarity - In the outgroup species, the apex of the carapace is located at the level of the third vertebral scute. This state is considered plesiomorphic.

States - 0 = third vertebral scute
1 = second vertebral scute
? = intraspecifically variable

30. Well developed costo-peripheral fontanelles present

Variation - Costo-peripheral fontanelles are holes in the shell located along the sutures between the costal and peripheral plates. Though typically present in young turtles, they fuse by maturity in most species. Adult males of the kachuga group, Batagur, and Callagur retain large, conspicuous costo-peripheral fontanelles. These are relatively small or completely closed in adults of the pangshura group, Hardella, and Morenia.

Polarity - In the outgroup species, costo-peripheral fontanelles are absent in adults. This state is considered plesiomorphic.

States - 0 = costo-peripheral fontanelles small or absent
1 = costo-peripheral fontanelles pronounced

Epidermal Characters

31. Number of claws on manus (Boulenger, 1889)

Variation - First described by Boulenger (1889). Batagur is unique among this group in having a four-clawed manus. All other ingroup species have five claws on the manus.

Polarity - In the outgroup species, there are five claws on the manus. This state is considered plesiomorphic.

States - 0 = five

1 = four

32. Extreme seasonal and sexual dichromatism

Variation - Batagur, Callagur, and two members of the kachuga group (K. kachuga and K. trivittata) exhibit extreme seasonal and sexual dichromatism. The remaining member of the kachuga group (K. dhongoka), the pangshura group, Hardella, and Morenia lack pronounced dichromatism.

In Callagur, females have brown heads and shells, while males exhibit two color phases. The dark phase seems to occur primarily during the non-breeding season when males have a brown shell and a dark gray to black head with a dull orange stripe running midsagittally from the snout to the occipital region. The light phase appears to be associated with breeding and is characterized by a cream-colored shell and a white head with the dull orange stripe replaced by a bright scarlet stripe (Moll, et al., 1981)

In Batagur, females have a brown iris and greenish gray to bluish gray skin and shell, while non-breeding males are slightly darker and have a cream colored iris. In contrast, breeding males have jet black skin and shells and completely white irises (Moll, 1978, 1985).

In K. trivittata, females are greenish-olive while males possess a yellow shell and neck and a red head with a midsagittal black stripe extending posteriorly from the nostrils (Theobald, 1868; in Moll, 1985).

Finally, in K. kachuga, females are dark brown to

black with the exception of a pale yellow plastron and silvery to pale yellow mandibles. In contrast, the males are brightly colored. While the carapace is drab olive and the plastron cream to light yellow, the head and neck are vividly patterned. The head is blue-black with a "broad geranium red patch extending from top of snout to occiput." The creamy white ground color of the neck is broken by six bright stripes, four of which converge with the red patch at the occiput. In addition, there are two sulfur yellow stripes on each side of the head and an orange oval spot on each side of the creamy-white throat. The iris and sclera of the eye are orange (Moll, 1986).

Polarity - The outgroup species does not exhibit extreme seasonal and sexual dichromatism. This state is considered plesiomorphic.

States - 0 = lack dichromatism

1 = dichromatism exhibited

33. Number of carapacial stripes

Variation - All members of the pangshura group possess a single median carapacial stripe, while two members of the kachuga group (K. dhongoka and K. trivittata), Callagur, and Hardella possess three carapacial stripes (one medial and two lateral). Finally, the carapaces of Morenia, Batagur, and Kachuga kachuga are not striped.

Polarity - In the outgroup species, the carapace is not striped. This state is considered plesiomorphic.

States - 0 = no stripes

1 = 1 stripe

2 = 3 stripes

Penial Morphology

34. Penis type

Variation - In all the ingroup species except Morenia, the penial morphology is such that the lateral folds of the plica media are characterized by having distinctively pointed distal flaps. This condition is referred to as the "flap type" penis. However, the lateral folds of the plica media as found in Morenia lack the pointed shape (Fig. 1).

Polarity - In the outgroup species, the penis is not a flap type. This state is considered plesiomorphic.

States - 0 = lacking flaps

1 = flap type

35. Medial fold of plica media

Variation - In all members of the ingroup except Morenia, the medial fold of the plica media is triangular in shape (Fig. 1).

Polarity - In the outgroup species, the medial fold of the plica media is triangular in shape. This state is considered plesiomorphic.

States - 0 = triangular-shaped

1 = not triangular-shaped

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- Figure 14. Best taxonomic arrangement for Batagur, Callagur, and Kachuga

Figure 1. Penial morphology. (A) Flap type penis of ingroup species as shown in Callagur borneoensis. (B) Non-flap type penis of outgroup species Ocadia sinensis. Note also the triangular-shaped inner fold of the plica media in both. Scale marker represents 5 mm.

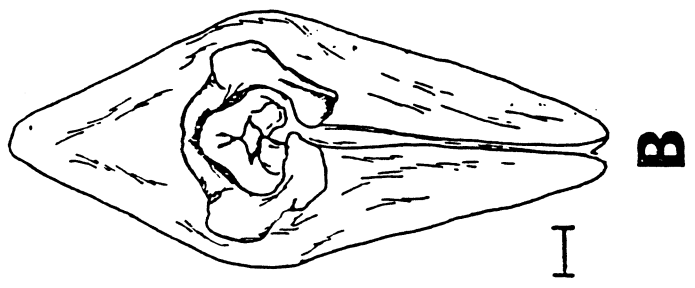
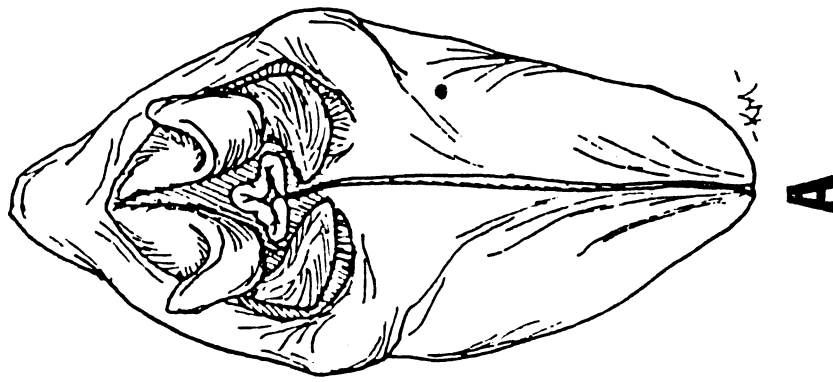
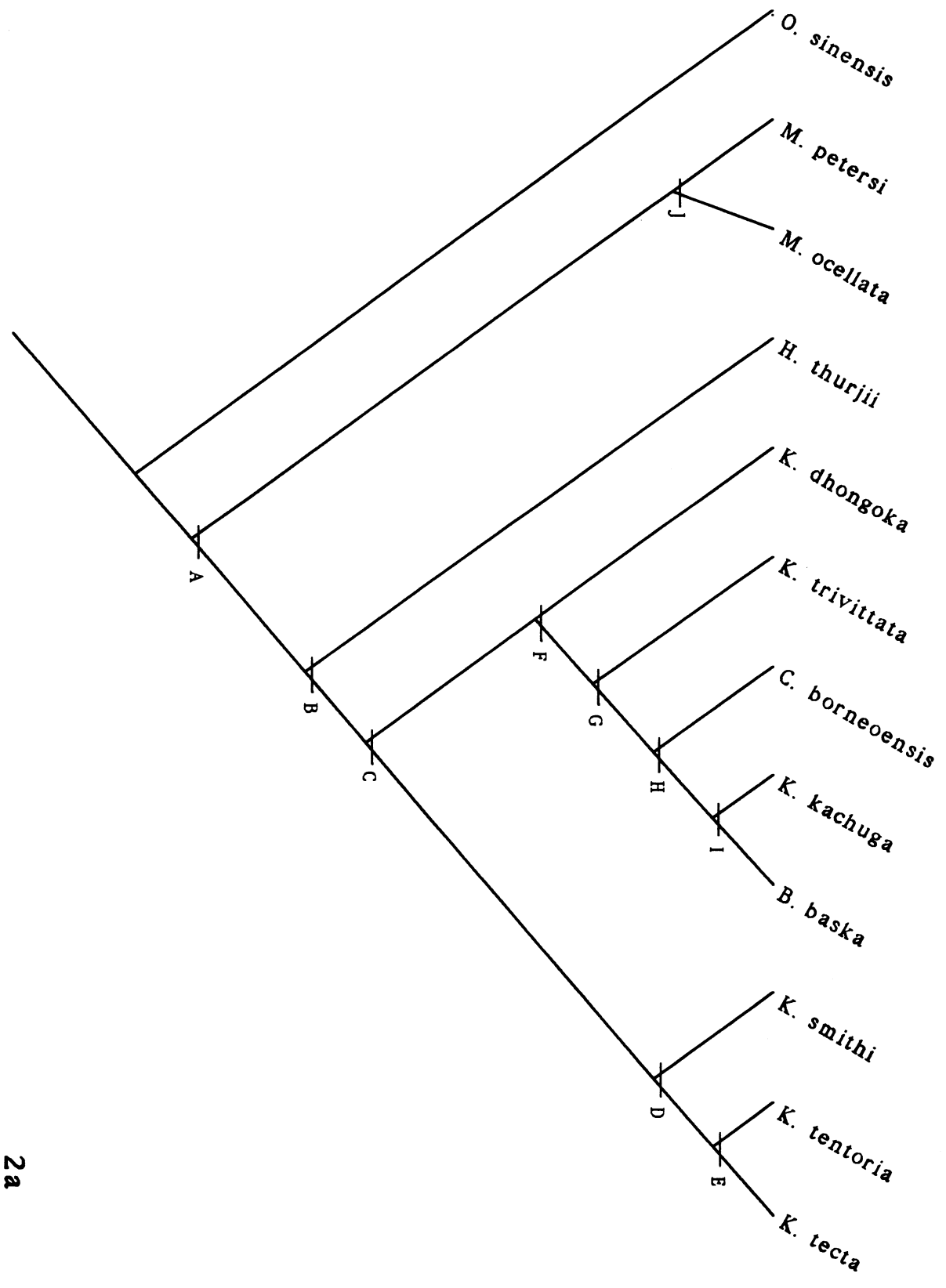


Figure 2. Cladograms for the 12 study species based on phylogenetic analysis of 35 characters using the PAUP computer program. The letters at each node denote the set of characters which diagnose that node. The corresponding groups of characters are listed on the page following each cladogram.



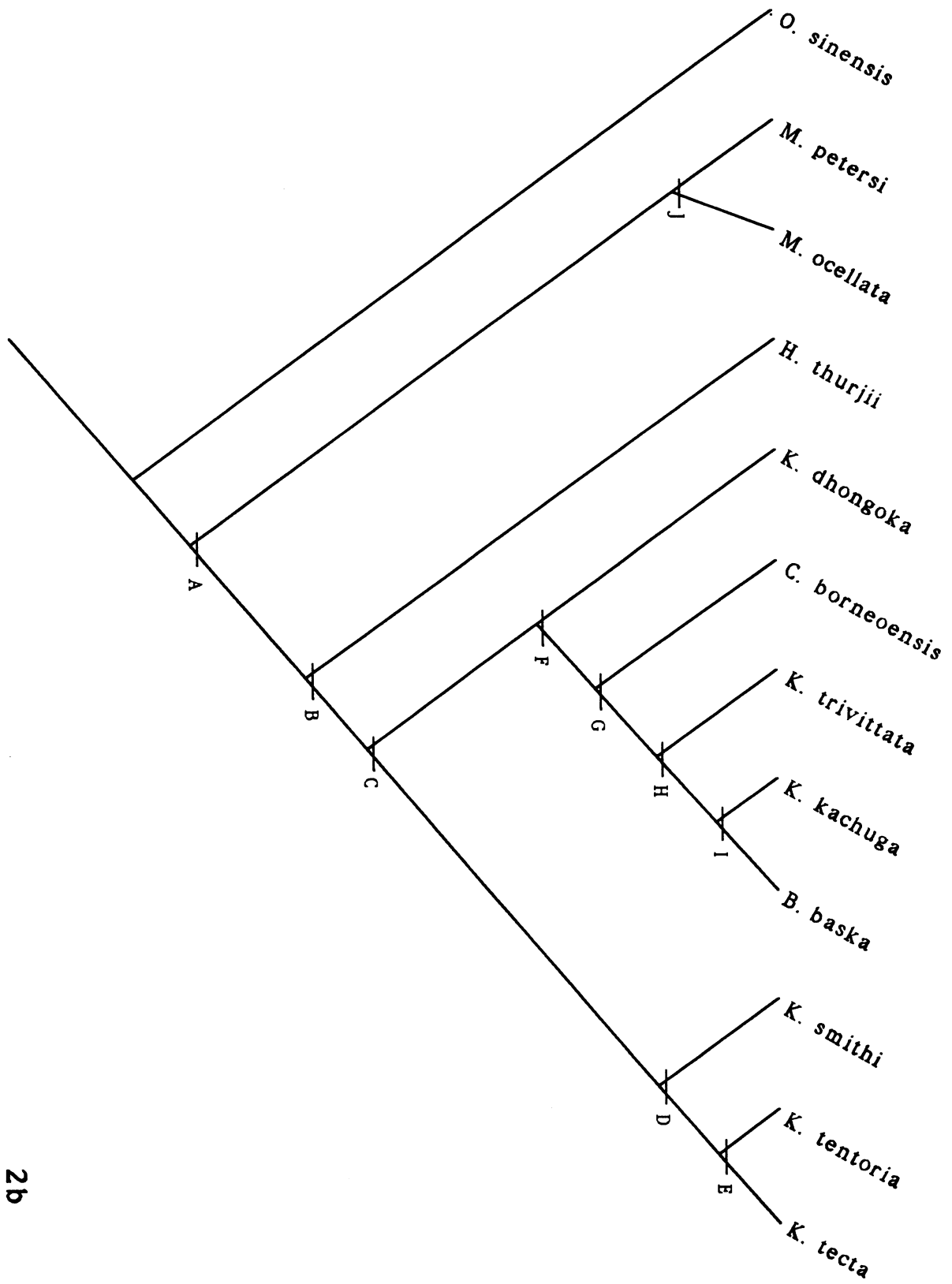
Character groups for cladogram 2a.

The characters diagnosing each node are listed under the node. Reversals (R) and homoplasies (H) are noted.

<u>Node A</u>	<u>Node B</u>	<u>Node C</u>	<u>Node D</u>	<u>Node E</u>
4	8	4 (R)	1	20
7	33	15 (R)	19 (R in <u>K. tecta</u>)	28
11	34	24	22	
13		25	23	
15			33	
16				
17				
18				
24				
25				
26				

<u>Node F</u>	<u>Node G</u>	<u>Node H</u>
12	4	24 (R)
29	14 (H with <u>H. thurjii</u>)	25 (R)
30	32	

<u>Node I</u>	<u>Node J</u>
3 (H with <u>K. dhongoka</u>)	2
14	3 (H with <u>B. baska</u>)
15	5
33 (R)	9
	14
	26
	27
	35



2b

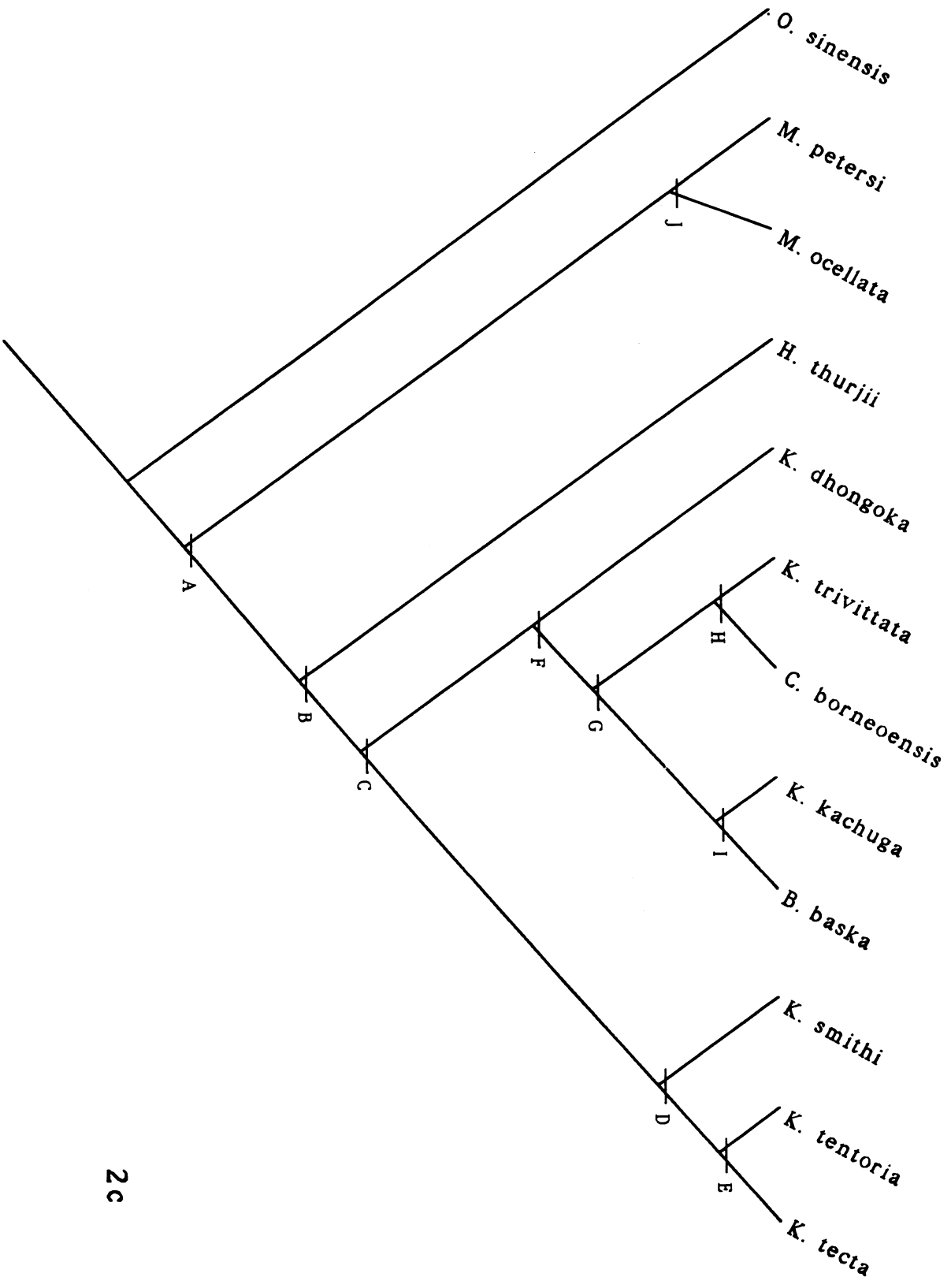
Character groups for cladogram 2b.

The characters diagnosing each node are listed under the node. Reversals (R) and homoplasies (H) are noted.

<u>Node A</u>	<u>Node B</u>	<u>Node C</u>	<u>Node D</u>	<u>Node E</u>
4	8	4 (R)	1	20
7	33	15 (R)	19 (R in <u>K. tecta</u>)	28
11	34	24	22	
13		25	23	
15			33	
16				
17				
18				
24				
25				
26				

<u>Node F</u>	<u>Node G</u>	<u>Node H</u>
12	4	zero length branch
29	14 (H with <u>H. thurjii</u>)	
30	32	

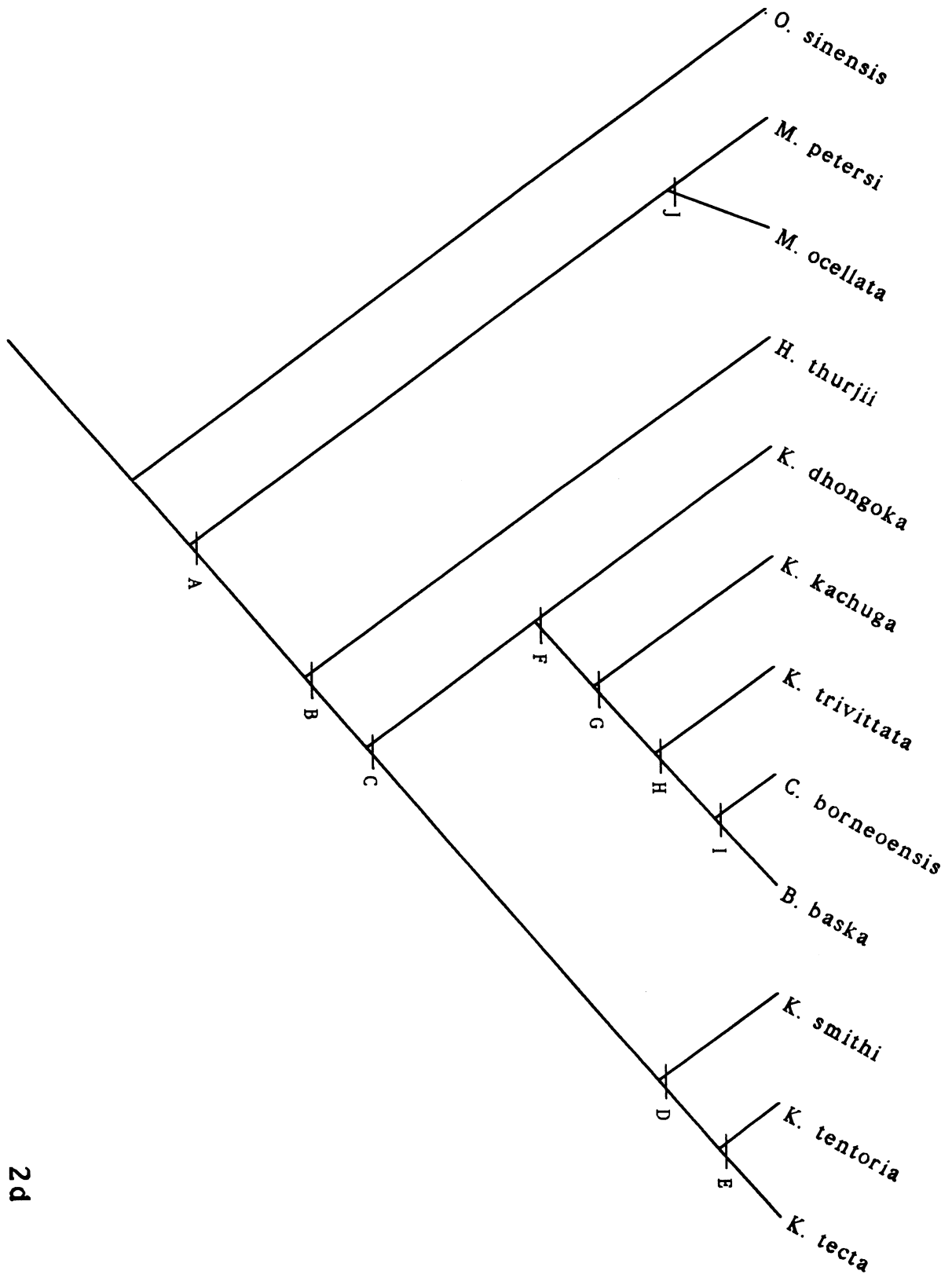
<u>Node I</u>	<u>Node J</u>
3 (H with <u>K. dhongoka</u>)	2
14	3
15	5
33	9
	14
	26
	27
	35



Character groups for cladogram 2c.

The characters diagnosing each node are listed under the node. Reversals (R) and homoplasies (H) are noted.

<u>Node A</u>	<u>Node B</u>	<u>Node C</u>	<u>Node D</u>	<u>Node E</u>
4	8	4 (R)	1	20
7	33	15 (R)	19 (R in <u>K. tecta</u>)	28
11	34	24	22	
13		25	23	
15			33	
16				
17				
18				
24				
25				
26				
<u>Node F</u>	<u>Node G</u>	<u>Node H</u>		
3	4	3 (R)		
12	14	14 (H with <u>H. thurjii</u>)		
29	32			
30				
<u>Node I</u>	<u>Node J</u>			
15	2			
33	3 (H with <u>B. baska</u>)			
	5			
	9			
	14			
	26			
	27			
	35			



Character groups for cladogram 2d.

The characters diagnosing each node are listed under the node. Reversals (R) and homoplasies (H) are noted.

<u>Node A</u>	<u>Node B</u>	<u>Node C</u>	<u>Node D</u>
4	8	4 (R)	1
7	33	15 (R)	13 (H with Nodes J & H)
11	34	24	19
15		25	22
16			23
17			33
18			
24			
25			
26			

<u>Node E</u>	<u>Node F</u>	<u>Node G</u>	<u>Node H</u>
20	3	4	3 (R)
28	12	14	13 (H with Nodes D & J)
	29	32	14 (H with <u>H. thurjii</u>)
	30		

<u>Node I</u>	<u>Node J</u>
24	2
25	3 (H with <u>B. baska</u>)
	5
	9
	13 (H with Nodes D & H)
	14
	26
	27
	35

Figure 3. Consensus tree based on four cladograms in
Figure 2a-d.

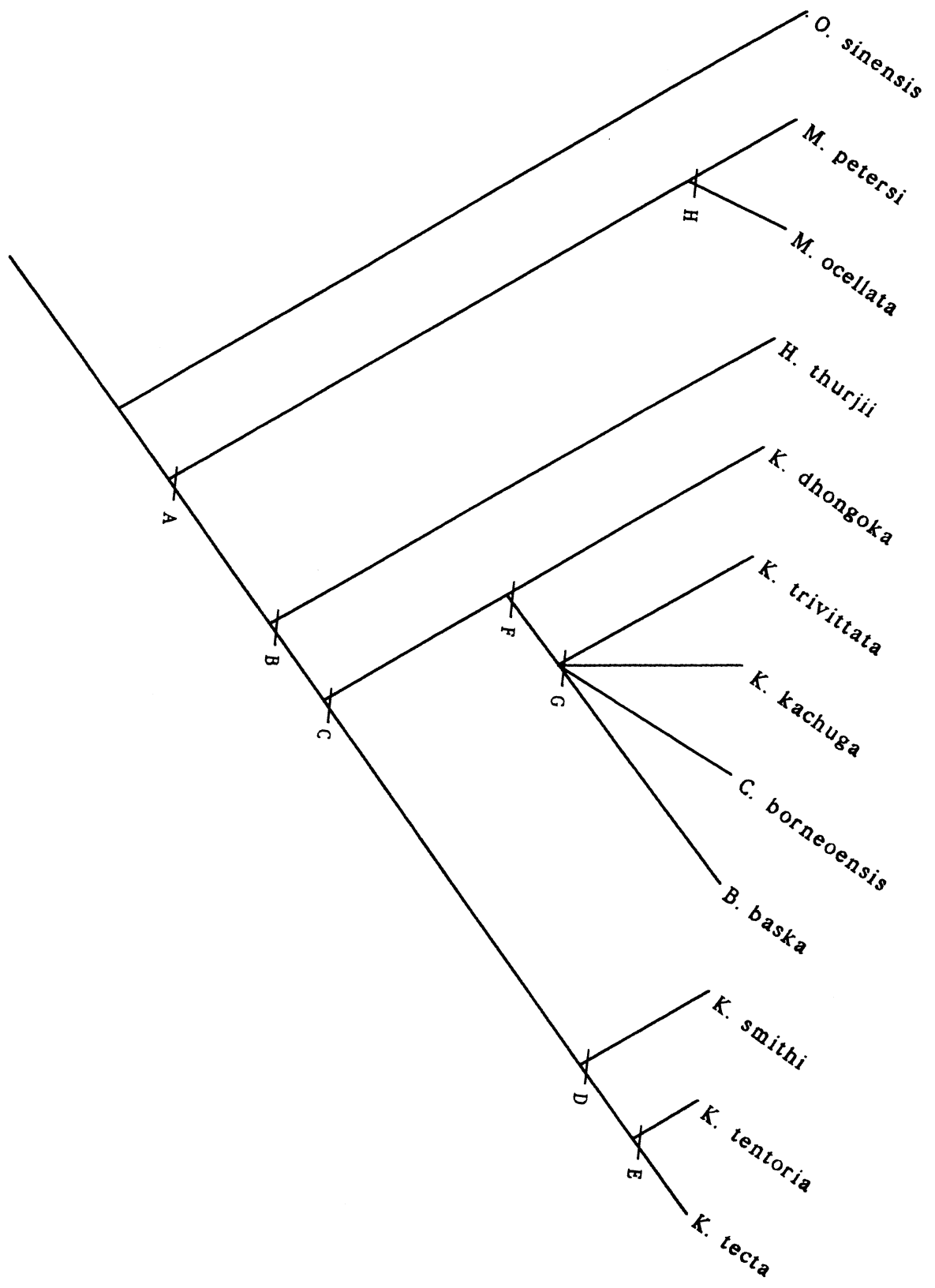
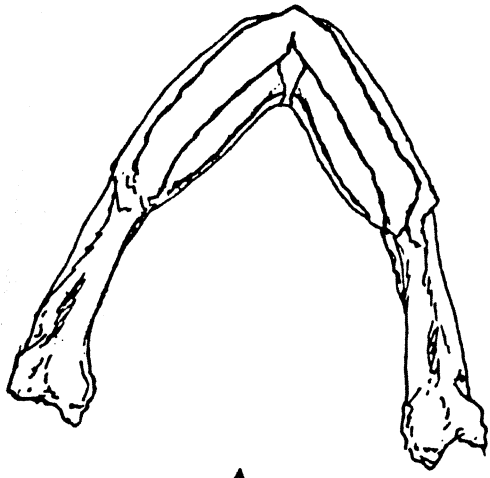
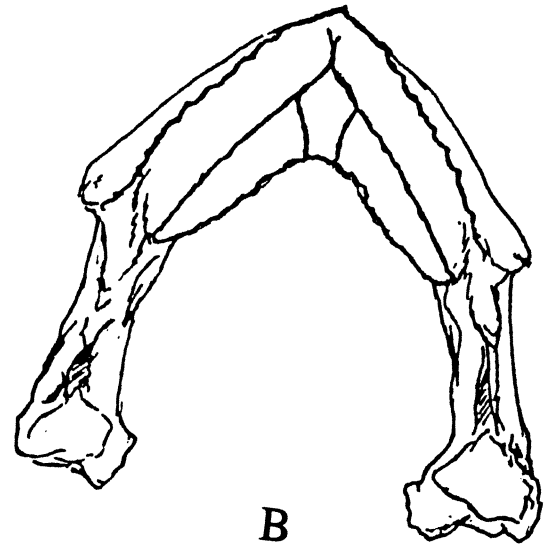


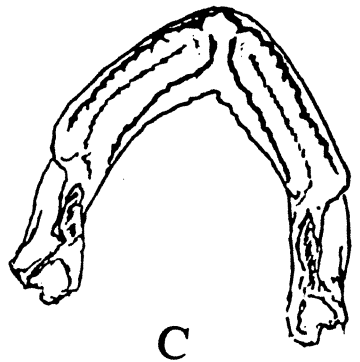
Figure 4. Pattern of ridges on the lower jaw of Batagur baska (A), Kachuga kachuga (B), Hardella thurjii (C), Kachuga dhongoka (D), K. tentoria (E), and Callagur borneoensis (F). Scale marker represents 1 cm.



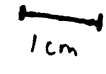
A



B



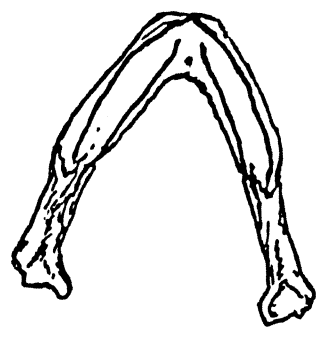
C



D



E



F

Figure 5. Anterior view of the heads of Kachuga kachuga (A) and K. tentoria (B). Note the medial notch in A and its absence in B. Scale marker represents 1 cm. (From Moll, 1986, p. 543).

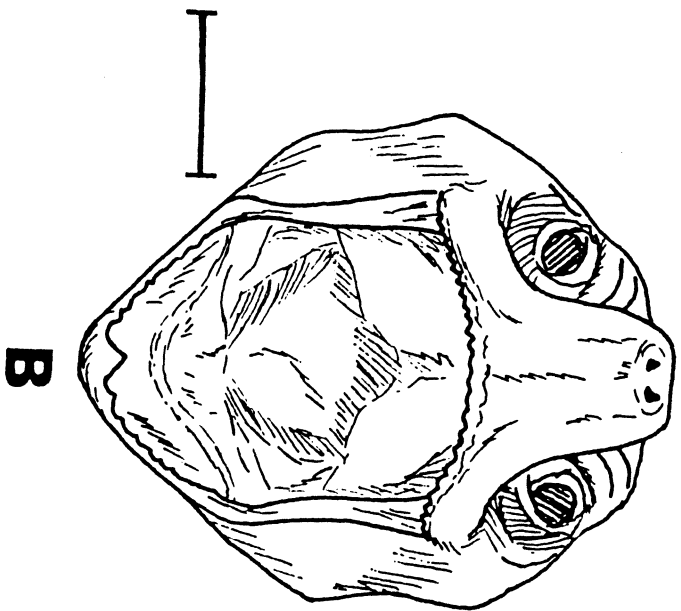
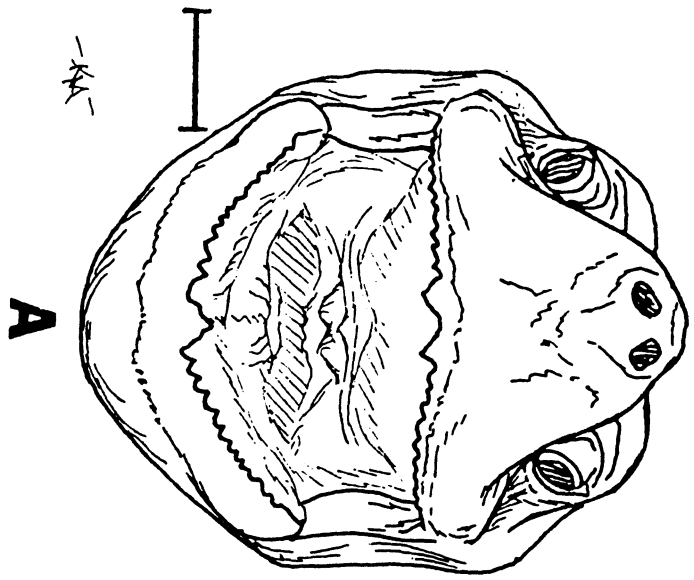


Figure 6. Vertebral scutes of Kachuga dhongoka (A) and K. tentoria (B). Arrow denotes broad contact between the third and fourth vertebral scutes in A but narrow contact in B. (From Moll, 1986, p. 546).

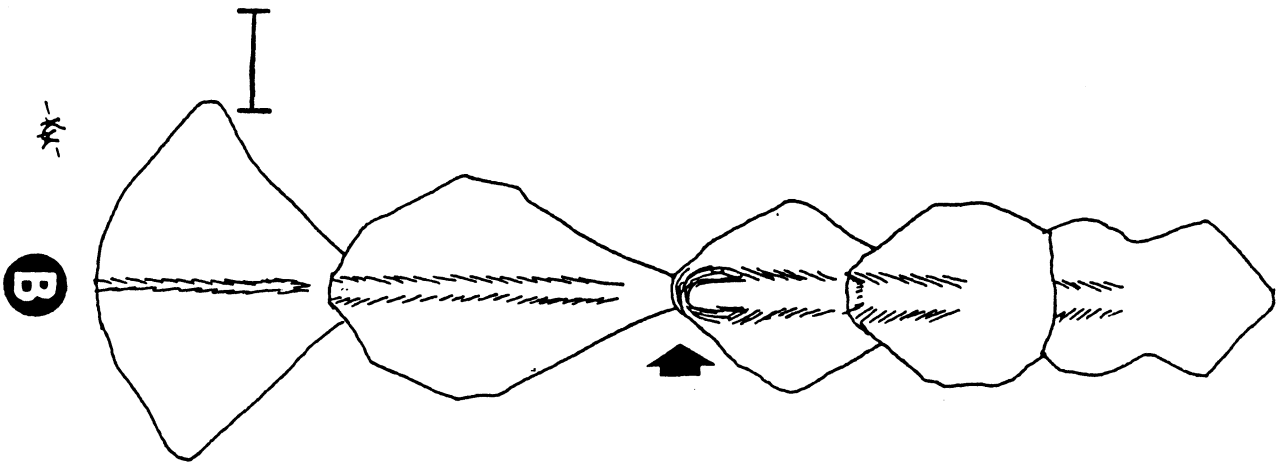
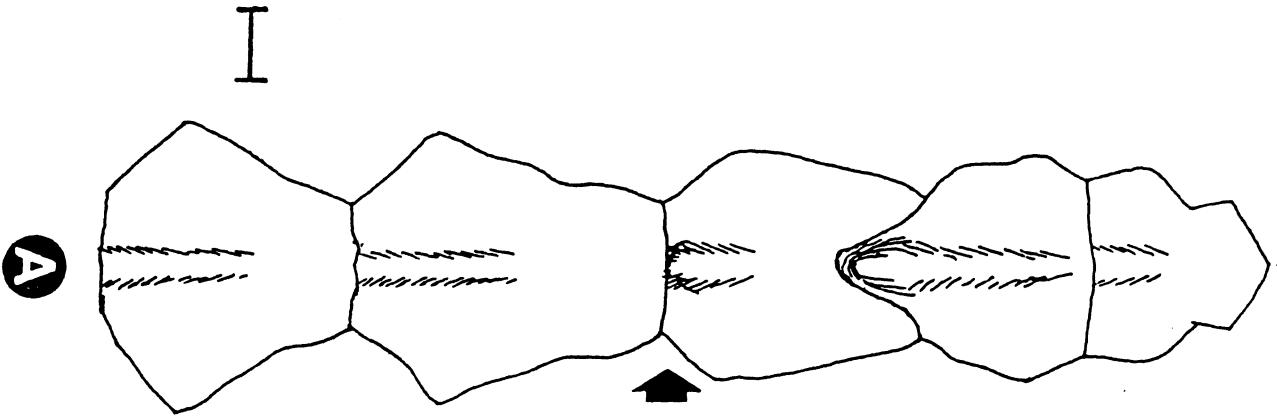


Figure 7. Neural bones of Kachuqa dhongoka (A) and K. tentoria (B). Arrow indicates six-sided and eight-sided fourth neural (From Moll, 1986, p. 544).

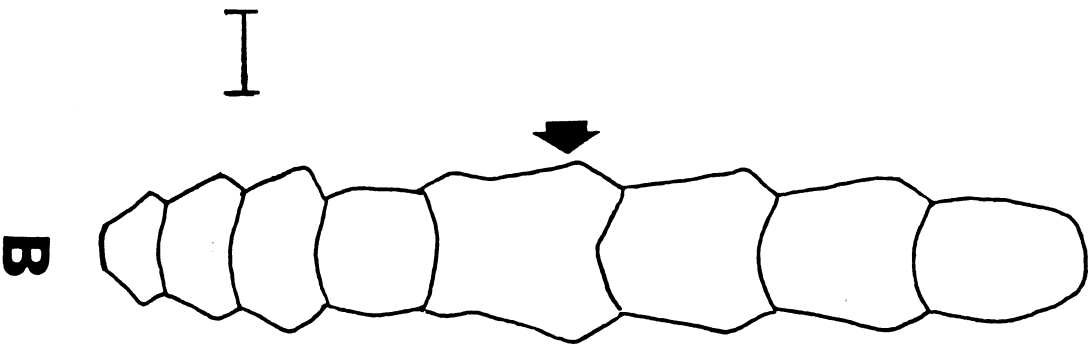
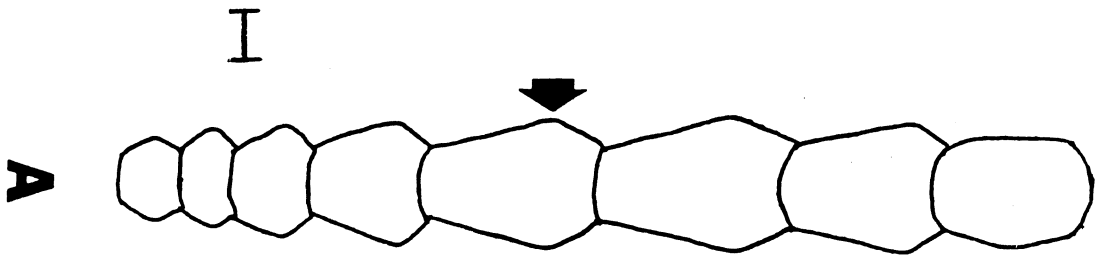
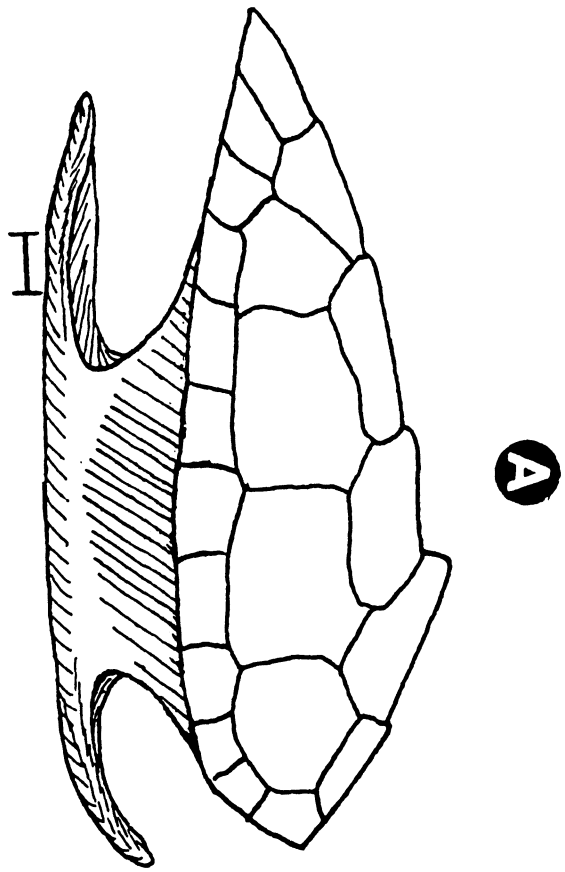
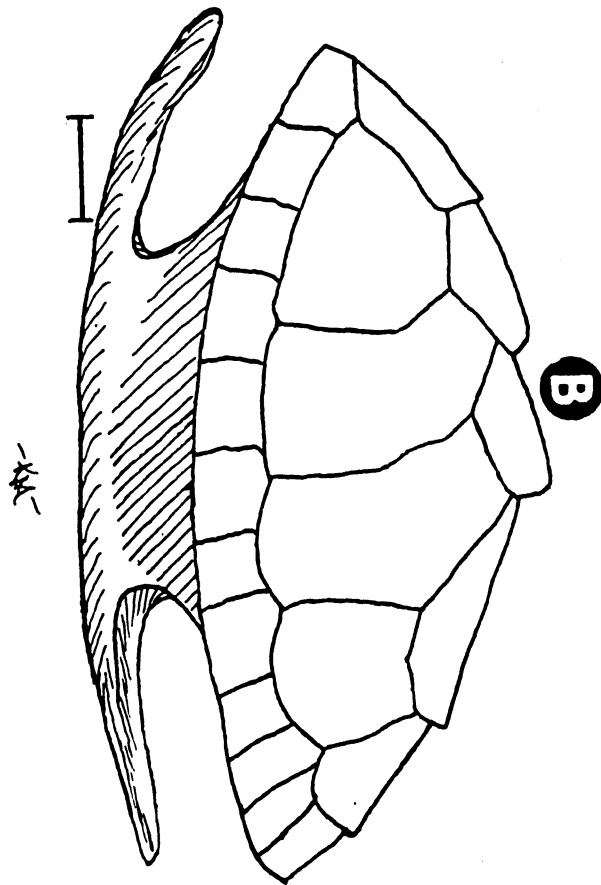


Figure 8. Shells of Kachuqa dhongoka (A) and K. tentoria (B). Note that the apex of A is at the level of the second vertebral scute and that of B is at the level of the third vertebral. (From Moll, 1986, p. 545).



A



B

Figure 9. Shell of a Kachuga dhongoka male with scutes removed to show large costoperipheral fontanelles. (From Moll, 1986, p. 547).

1 cm

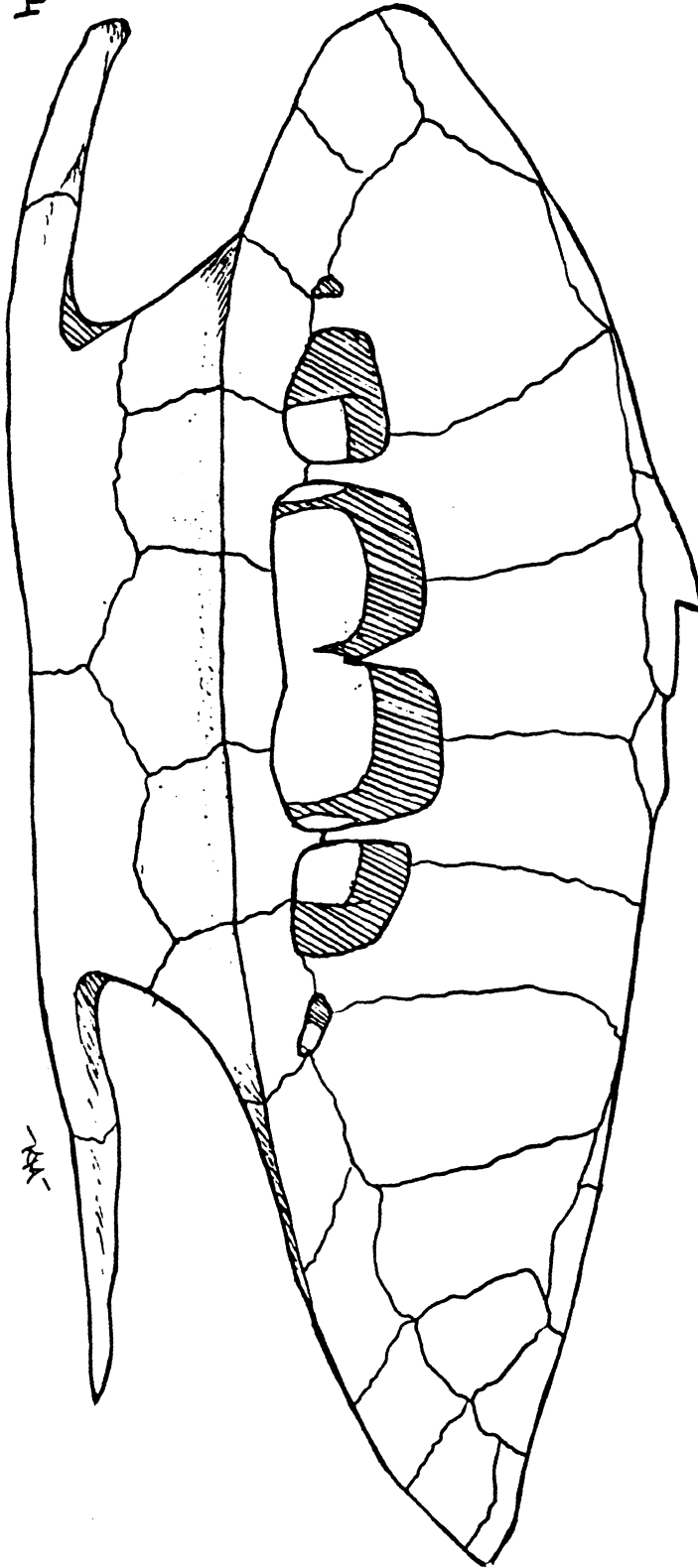


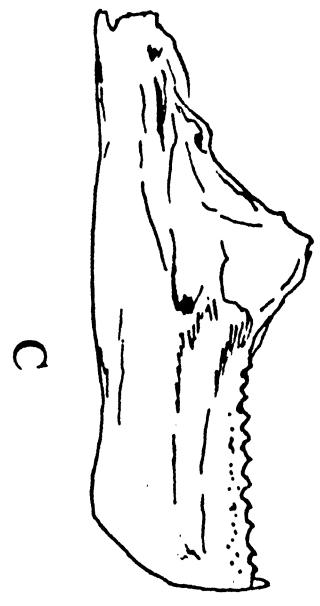
Figure 10. Elevation of the coronoid process of the dentary (lateral view) of Batagur baska (A), Callagur borneoensis (B), and Kachuga kachuga (C). Note the low elevation of A, the moderate elevation of B, and the high elevation of C. Scale marker denotes 1 cm.



A



B



C

Figure 11. Pattern of ridges on the upper jaw of Callagur borneoensis (A) and Batagur baska (B). Note the double alveolar ridge (denoted by arrow 1) and anterior parasagittal ridges (denoted by arrow 2) of (B) and the single alveolar ridge and lack of anterior parasagittal ridges of (B). Scale marker represents 1 cm.

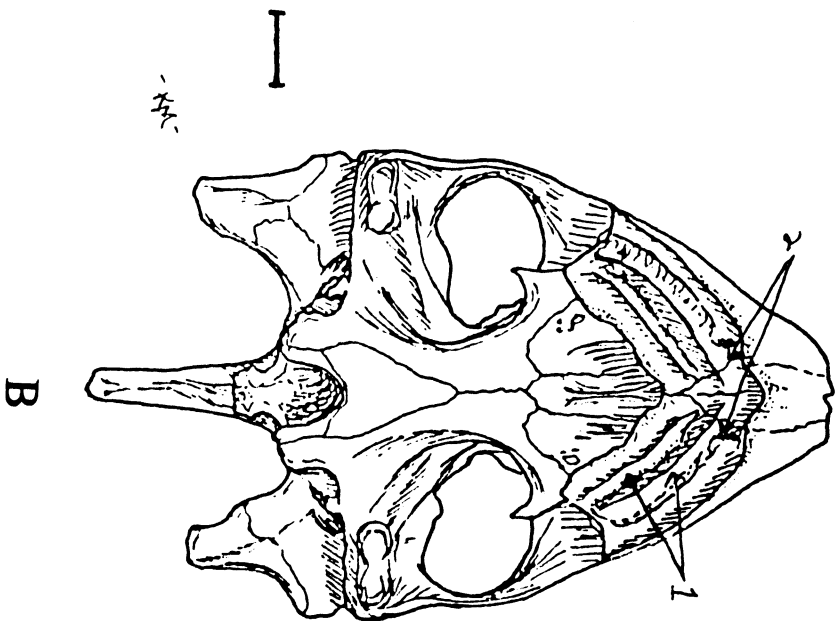
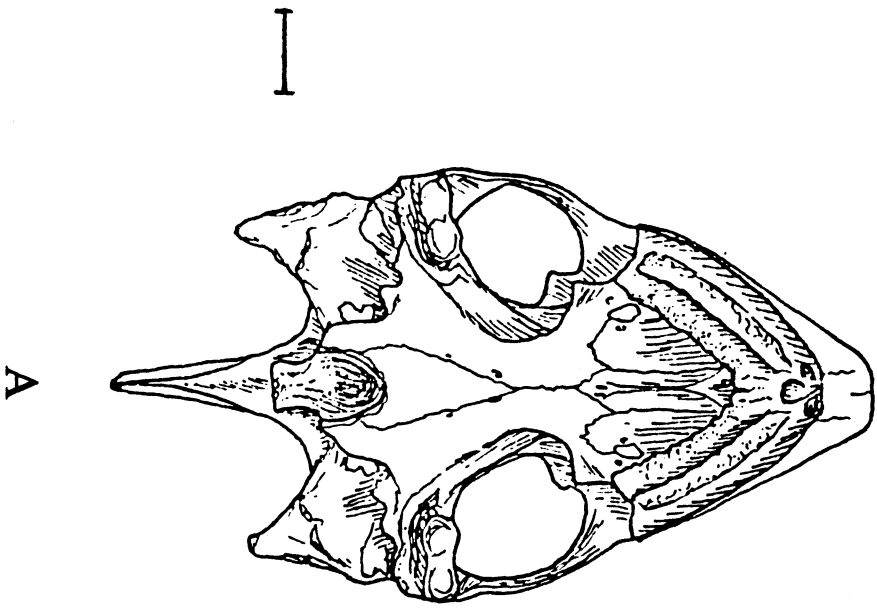


Figure 12. Hirayama's (1984) arrangement of taxa. Note that Kachuga kachuga and K. dhongoka are not included in this analysis.

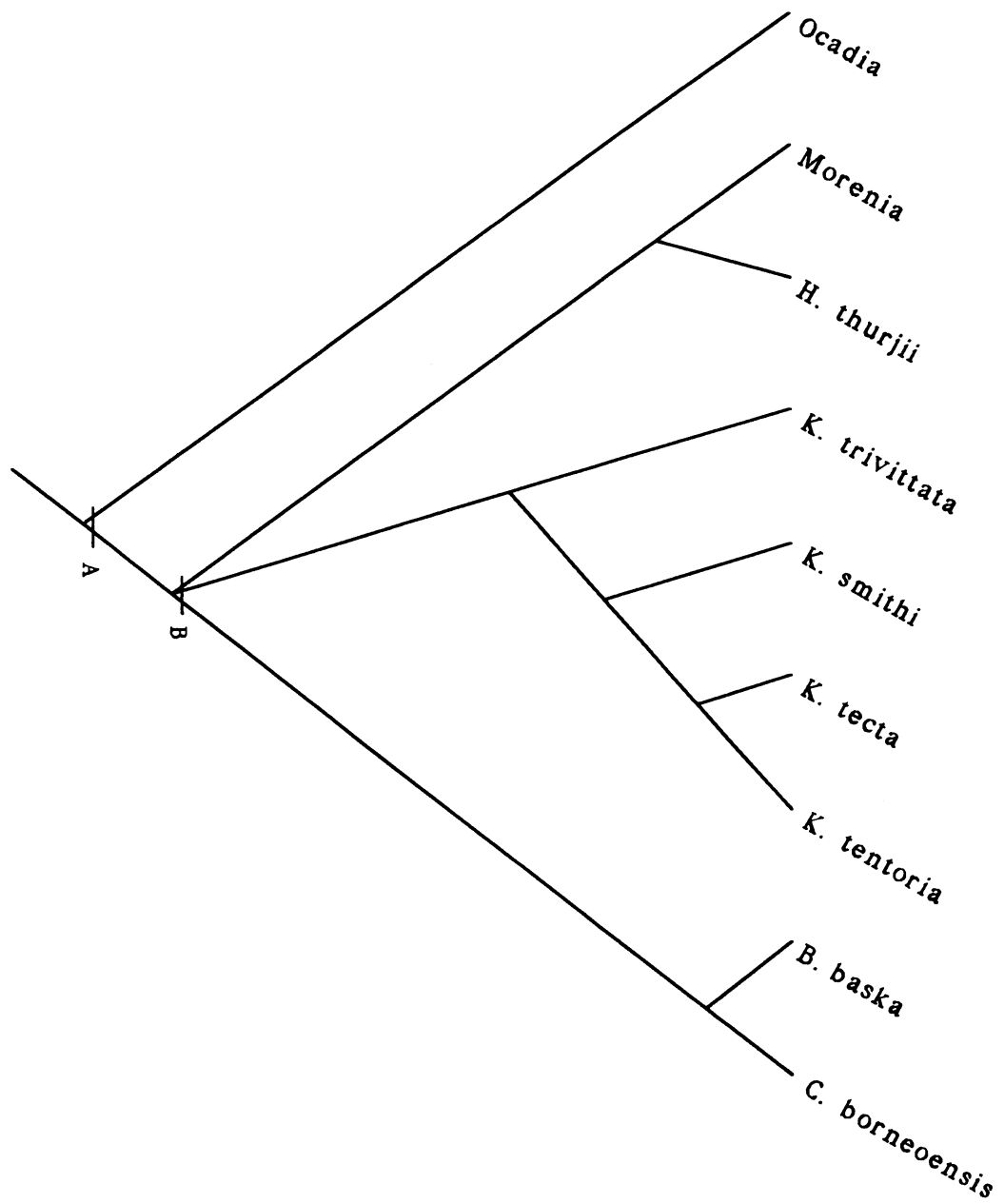


Figure 13. One possible taxonomic arrangement for the taxa previously classified as Batagur baska, Callagur borneoensis, Kachuqa kachuqa, K. dhongoka, K. trivittata, K. smithi, K. tecta, and K. tentoria.

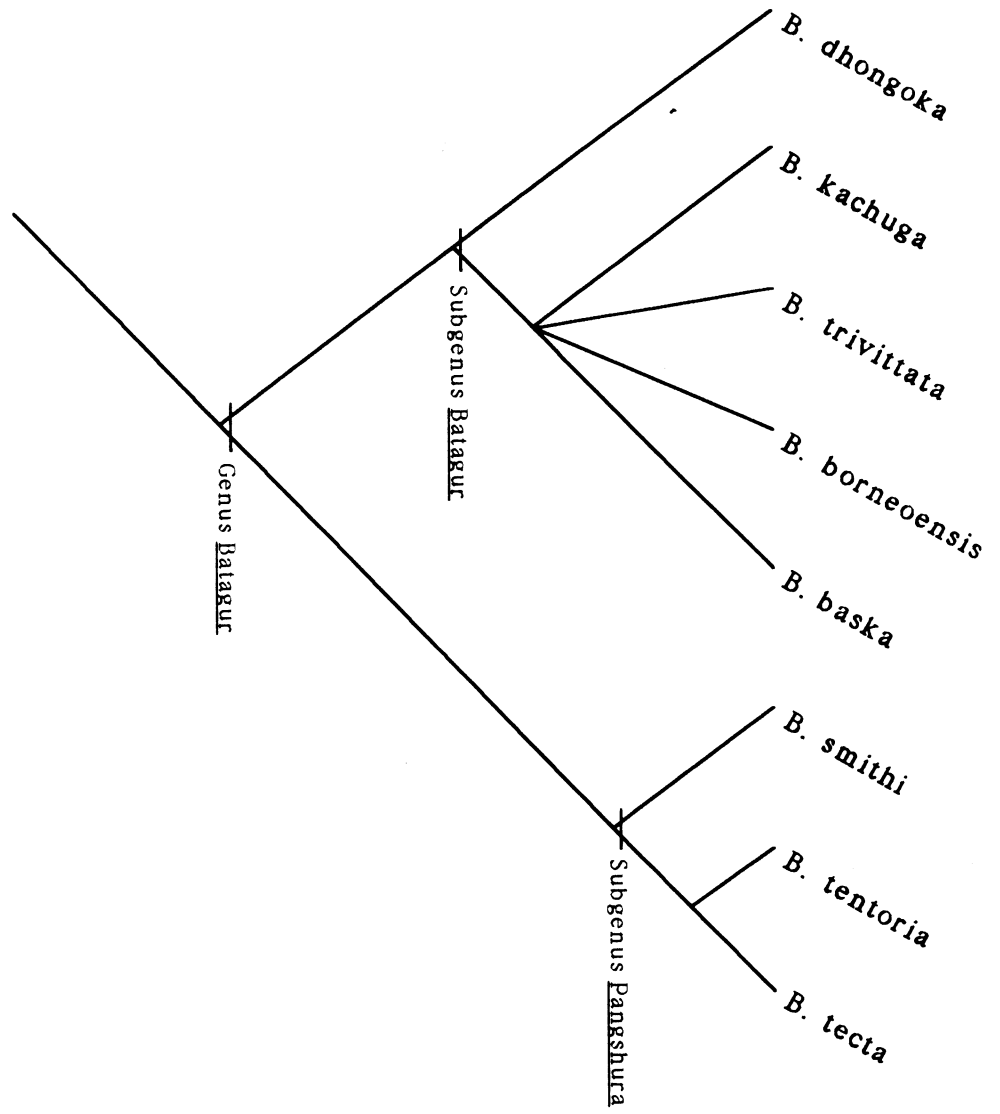


Figure 14. Cladogram showing the relationships within the Batagur and Pangshura genera.

