Wallago Bleeker, 1851 and *Wallagonia* Myers, 1938 (Ostariophysi, Siluridae), Distinct Genera of Tropical Asian Catfishes, with Description of †*Wallago maemohensis* from the Miocene of Thailand

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ABSTRACT

The Southeast Asian silurid catfish genus *Wallagonia* Myers, 1938, although regarded as a junior synonym of *Wallago* Bleeker, 1851 by recent authors following Myers (1948), differs fundamentally from it in many external and osteological characters. The genera evidently have been distinct since at least the middle Miocene and apparently are not closely related to each other. *Wallagonia* seems most similar to the silurid genus *Ompok*. *Wallago* differs most strikingly from all other silurids in having a much longer gape, extending ventroposteriorly well beyond the eyes. The extremely elongate upper jaw has a unique bony composition and suspension. It consists of three bones: the toothed premaxillary bone anteriorly, and the toothless suborbital and first postorbital bones posteriorly. The premaxillary bone is partially suspended from the cranium by the infraorbital bone. The closest relatives of *Wallago* have not been identified. *Wallagonia* and *Wallago* have no previously reported fossil records. Fossils of the family Siluridae have been identified as representatives of the Eurasian temperate genus *Silurus* (Kobayakawa, 1989). Here an extinct species of *Wallago* is described, *W. maemohensis*, on the basis of a complete cranium with attached, fully toothed left premaxillary in an unusually fine state of preservation from a Miocene deposit near Lampang in northern Thailand. Fossil catfishes previously reported from Thailand belong to the families Bagridae and Pangasiidae and are from Pliocene deposits (Roberts and Junmongthai 1999).

KEYWORDS

Catfishes, Siluridae, *Wallago attu*, *Wallagonia leerii*, *Wallago maemohensis*, Miocene, Thailand

Introduction

Siluridae is an exclusively Eurasian family of primary freshwater catfishes. About 15 genera and 100 living species are recognized. Some of these are giants among the catfishes, attaining 1, 2, 3 or reportedly up to 5 m in length, and weights of as much as 300 kg. The greatest taxonomic diversity occurs in tropical Asia, including the Chao Phraya and Mekong basins, Malay Peninsula, Sumatra and Borneo. The few fossil silurids reported until now, from Europe and Japan, seem to be congeners of the temperate genus *Silurus*.

The silurid genus *Wallago* Bleeker, 1851, as recognized up to now, comprises the following nominal taxa, all living (Eschmeyer [2014]):

Silurus attu Bloch and Schneider, 1801: type locality Malabar, India

Silurus boalis Hamilton, 1822: type locality Ganges

Silurus wallagoo Valenciennes in Cuvier and Valenciennes, 1840: type localities Coromandel, Calcutta, and Vizagapatam, India; Myanmar

Silurus muelleri Bleeker, 1846: type locality Jakarta, Indonesia

Wallago leerii Bleeker, 1851: type localities Sambas, western Borneo; Palembang, southern Sumatra, Indonesia

Wallago russellii Bleeker, 1853: type localities Calcutta, India; Jakarta, Indonesia

Wallago nebulosus Vaillant, 1902: type locality Tepoe, Mahakam River, Borneo

Wallagonia tweediei Hora and Misra, 1941: type locality Kuala Tahan, Pahang, Malaysia

Wallago attu valeya Deraniyagala: type locality Yakvala, Sri Lanka

Wallago maculatus Inger and Chin, 1959: type locality Kinabatangan River at Deramakot Forest Reserve, Sabah, Malaysia

Wallago micropogon Ng, 2004: type locality Stung Treng, Cambodia (Mekong basin)

Silurus muelleri is the type species of the genus *Wallago* (Kottelat 2013:239). *Wallago muelleri* has been regarded consistently as a junior synonym of *W. attu,* but this has not been substantiated by direct comparison of specimens from their respective type localities in India and Java. Specimens identified as *W. attu* from India and Thailand differ in osteological details. Material identifiable as *W. muelleri*, which might also be osteologically distinctive, has not been available for this study.

Silurus boalis*, *S. wallagoo*, *Wallago russellii* and *W. attu valeya* also are currently regarded as junior synonyms of *W. attu*.

Wallago leerii, recognized as a valid species since its description, is the type species by original designation of the nominal genus *Wallagonia* Myers, 1938. *Wallagonia* was placed by Myers (1948) and nearly all subsequent authors as a junior synonym of *Wallago*, but it is here recognized as a distinct genus. *Wallago nebulosus* and *Wallagonia tweediei* are currently recognized as synonyms of *Wallago leerii*. It is doubtful that *Wallago maculatus* and *Wallago micropogon* are distinct species; they are distinguished largely on the basis of coloration and presumably do not differ greatly in osteology.

In proposing his new genus *Wallagonia* as distinct from *Wallago*, Myers (1938) was dealing only with a seemingly simple problem of nomenclatural priority. Consequently, he did not provide characters to distinguish *Wallagonia* from *Wallago*. Ten years later, after discovering that his information on the date of original publication of the name *Wallago* had been incorrect, he declared that *Wallagonia* Myers, 1938 was a junior synonym of *Wallago* (Myers 1948). As he stated in 1948, however, material of *Wallago attu* was unavailable to him in 1938, and he had examined only *Wallago leerii*. For this reason *Wallago leerii* rather than *Wallago attu* was selected as the type

species of *Wallagonia. Wallagonia* is based therefore on *Wallago leerii*, a species fundamentally different in morphology and osteology from *Wallago attu*, as documented below.

Materials and Methods

This study is based mainly on dried skeletal preparations of medium-sized to large specimens of *Wallago* and *Wallagonia* and other silurids that I collected, prepared and deposited in the fish collection of the Thailand Natural History Museum of the National Science Museum in Pathumtani (THNHM-F). Specimen data are as follows:

Wallago attu: Cambodia, Kampong Thom, 1–6 September 2000, 5 specimens (THNHM-F-01545); Thailand, Pathumtani market, 21 March 1999, 960 mm (THNHM-F-01546).

Wallagonia leerii: Sumatra, Palembang market, 12 April 1999, 560 mm (THNHM-F-01547).

Wallagonia leerii (or *W. micropogon*): Mekong at Ban Wern Buk, northeast Thailand, 21 April 2000, 495 mm (THNHM-F-01548); northeast Thailand, July 2001, cranial length 100 mm (THNHM-F-01549).

Belodontichthys dinema: Sumatra, Musi basin, Hulu Rawas (Lubuk Linggau market), 28 April 1999, 505 mm (THNHM-F-01549).

Belodontichthys truncatus: Cambodia, Kratie, various dates, 5 complete skeletons, 3 with disarticulated skulls (THNHM-F-01550).

Micronema sp.: Thailand, Pathumtani market, 21 March 1999, 550 mm (THNHM-F-01551).

Silurus glanis: Austria, Vienna market, September 2001, 3 specimens, skulls, Weberian apparatus and pectoral girdle (THNHM-F-01552).

Silurus sp.: Vietnam, Tuyen Quanh market, 1999, 407 mm (THNHM-F-01553).

In addition to direct observation of the osteological material listed above, I have relied mainly on the well-illustrated account of the cranial osteology of Indian *Wallago attu* by Joseph (1960). Other works consulted for osteological information are Bornbusch (1991, 1995); Sinha (1959, 1962) and Tilak (1961). The fossilized cranium with one complete premaxillary bone attached to it, here described as *Wallago maemohensis*, was collected by me at Mae Moh coal mine in northern Thailand in 1998.

Character Distinctions

The two genera *Wallago* and *Wallagonia* are distinguished by the following characters (modified after Roberts 1982): *Wallago*—jaws extending posteriorly far beyond eyes; branchiostegal rays 18–21; total gill rakers on first gill arch 24–30; total anal fin rays 77–96; maxillary barbel usually extending posteriorly well beyond anal fin origin; mandibular barbel longer than pelvic fin. *Wallagonia*—jaws extending posteriorly only to below anterior border of eye; branchiostegal rays 12–19; total gill rakers on first gill arch 19 or fewer; total anal fin rays 60–75; maxillary barbel extending posteriorly no farther than anal fin origin; mandibular barbel shorter than pelvic fin.

Osteological Features

No other silurid has jaws extending posteriorly far beyond the eyes as in *Wallago*. The branchiostegal ray count of *Wallago* is higher than in any other silurid. According to Bornbusch (1995:9), "the maxillary barbel is flexible for its entire length" in all silurids except *Ceratoglanis*. The statement should also exclude *Wallago*. In this genus the maxillary bone is quite elongate. The base of the maxillary barbel is firmly attached to the distal two-thirds of the bone. The maxillary bone is highly mobile but rigid. Hence, the attached part of the barbel cannot be flexed. In *Wallagonia* the maxillary bone is much shorter, and apparently the maxillary barbel is attached quite near its tip, so virtually the entire barbel is flexible. *Ceratoglanis* and *Wallago* are not closely related: they represent extremely specialized silurids far apart from each other.

The skull and other osteological features of *Wallago attu* (Figures 1 and 3) and *Wallagonia leerii* (Figures 2 and 4) differ in so many ways and so profoundly that they are certainly distinct genera and probably diverged long ago, perhaps well before the Miocene. Bornbusch (1995) hypothesized that *Wallagonia leerii* is closely related to the South Asian and Southeast Asian silurid genus *Ompok*. He nevertheless identified the closest relative of *Wallagonia leerii* as *Wallago attu* by retaining them in the same genus. In a move long overdue, they are here separated into *Wallagonia* and *Wallago*, the genera of which they are the respective type species. A well-preserved cranium

and fully toothed upper premaxilla of *Wallago* I recently collected from a Miocene deposit in northern Thailand is described below as *Wallago maemohensis*.

Osteological Characters

Examination of the skeletal material listed above reveals that *Wallago* and *Wallagonia* differ in the following osteological characters.

MESETHMOID BONE
Wallago—relatively narrow, its wings moderately expanded (Figure 1); *Wallagonia*—relatively wide, its wings greatly expanded (Figure 2).

LATERAL ETHMOID BONES
Wallago—with long, narrow, and greatly extended lateral wings with two strongly projecting distal articular facets (Figure 1); *Wallagonia*—with short wings with single distal articular facet (Figure 2).

PREMAXILLARY BONES
Wallago—more than twice as long, extending posteriorly on side of head, to which they are strongly adpressed, attached to ventral surface of prevomer for only about one-sixth of their length (Figure 3); *Wallagonia*—short, transversely oriented, attached mainly to ventral surface of prevomer, beyond which they extend for only a short distance, less than one-third of their length (Figure 4).

PREMAXILLARY BONE SUSPENSION
Wallago—only in small part from prevomer, largely from highly modified third suborbital and the two postorbital bones, which in turn articulate with two articular facets on wing of lateral ethmoid (Figure 3); *Wallagonia*—exclusively from ventral surface of prevomer (Figure 4).

LOWER JAW OR MANDIBLE
(ANGULAR + DENTARY)
Wallago—moderately elongate (length 80% of cranial length); coronoid process higher (height 4.7 times in mandibular length) (Figure 3); *Wallagonia*—elongate (length 95% of cranial length), with a moderately low coronoid process (height 8.6 times in mandibular length) (Figure 4).

ATLAS CENTRUM
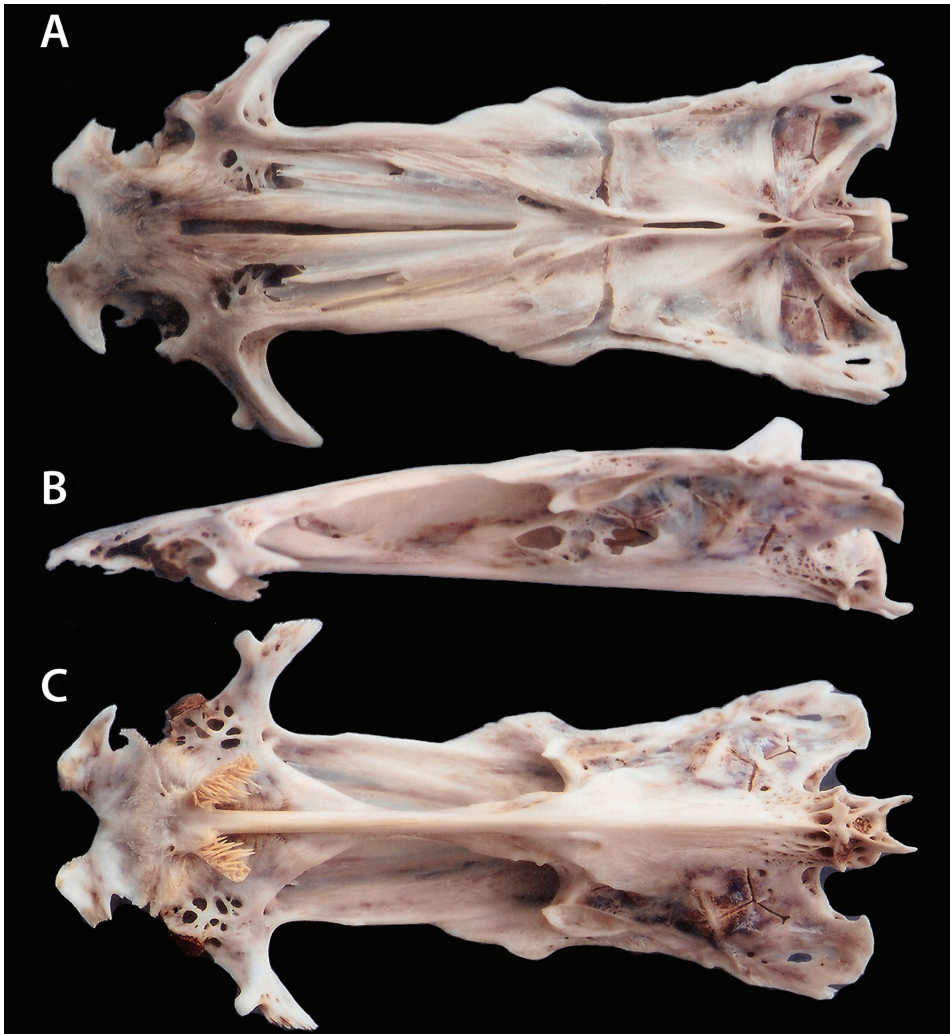*Wallago*—with anterior articular surface small and convex (opisthocoelous) (Tilak 1961:93–94,

FIGURE 1. *Wallago attu*, cranium. **A,** dorsal view. **B,** lateral view. **C,** ventral view. Mekong, cranial length 129 mm.

fig. 1); confirmed by me in specimens of different sizes); *Wallagonia*—with a very large concave (amphicoelous) articular surface.

FIRST POSTORBITAL BONE

Wallago—entirely laminar, with a distinctive horizontally oblong triangular shape, its long ventral margin loosely attached by connective tissue to dorsal margin of middle of suborbital bone, its posterior end widely separated from second postorbital bone (Figure 3); *Wallagonia*—tubular, with little or no laminar component, its anterior and posterior ends juxtaposed respectively to the preceding and succeeding suborbital and second postorbital bones (Figure 4).

PROCESSES FOR ATTACHMENT OF PREVOMERINE TOOTHPLATES

Wallago—highly raised from surface of prevomer, toothplates strongly oriented postero-obliquely (Figure 1C); *Wallagonia*—scarcely raised from surface of prevomer; prevomerine toothplates only slightly oriented postero-obliquely (Figure 2C).

DORSAL HALF OF CRANIUM

Wallago—with a very low-lying "double" crest (divided into two mediolateral crests) (Figure 1B); *Wallagonia*—with a greatly elevated median crest (of which only the posterior half is formed by the supraoccipital bone) (Figure 2B).
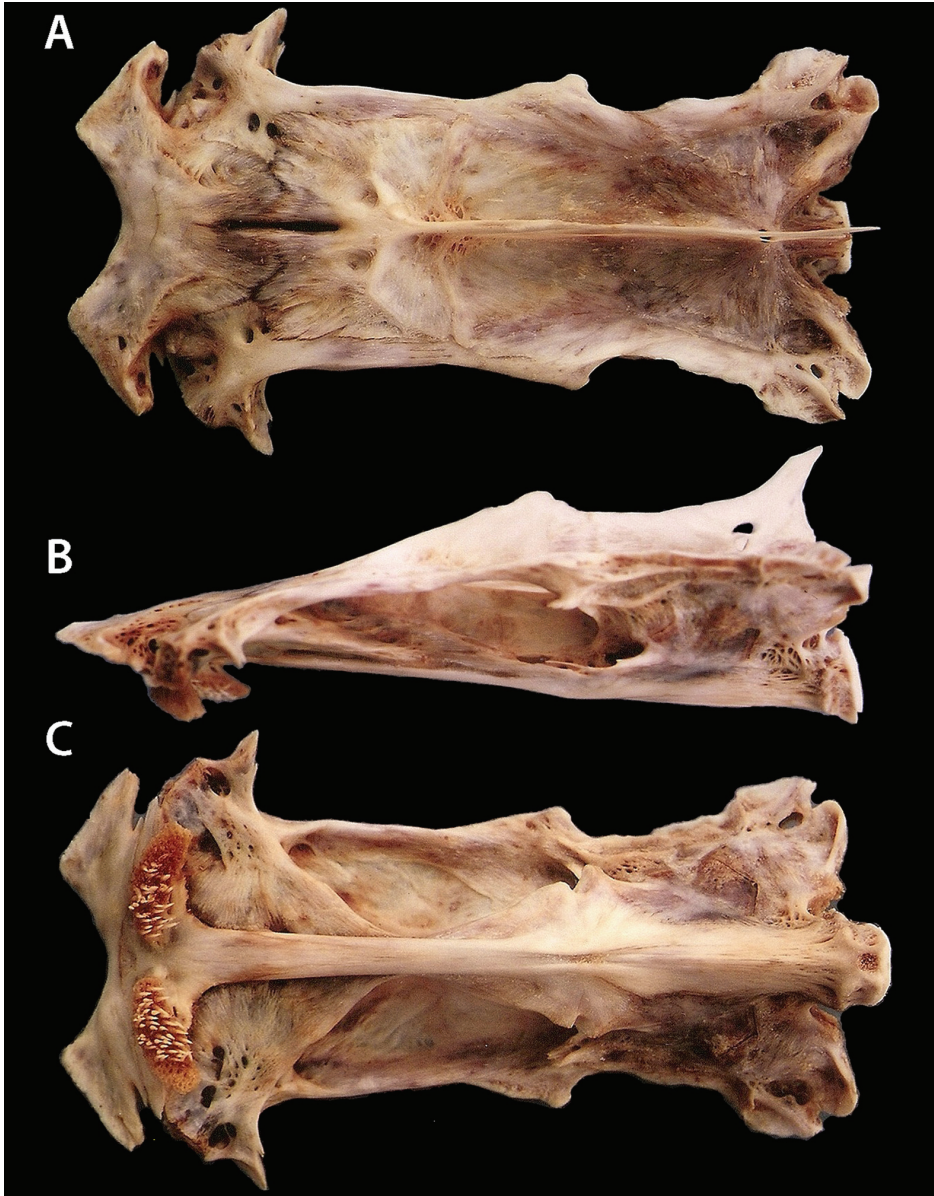
FIGURE 2. *Wallagonia leerii*, cranium. **A,** dorsal view. **B,** lateral view. **C,** ventral view. Mekong, cranial length 149 mm.

ANTERIOR CRANIAL FONTANEL
Wallago—very narrow and elongate, its length nearly half that of entire cranium (Figure 1A); *Wallagonia*—very narrow and short, its length only about one-seventh of cranial length (Figure 2A).

POSTERIOR CRANIAL FONTANEL
Wallago—narrow like anterior fontanel but very short, its length only about one-tenth of cranial length (Figure 1A); *Wallagonia*—absent or present as a vestigial structure between left and right halves of dorsal crest (Figure 2A).

FRONTAL BONES
Wallago—slender and separate, without dorsal crest, loosely joined together at midline by separate ventromedian crests arising on each bone and extending between anterior and posterior fontanels
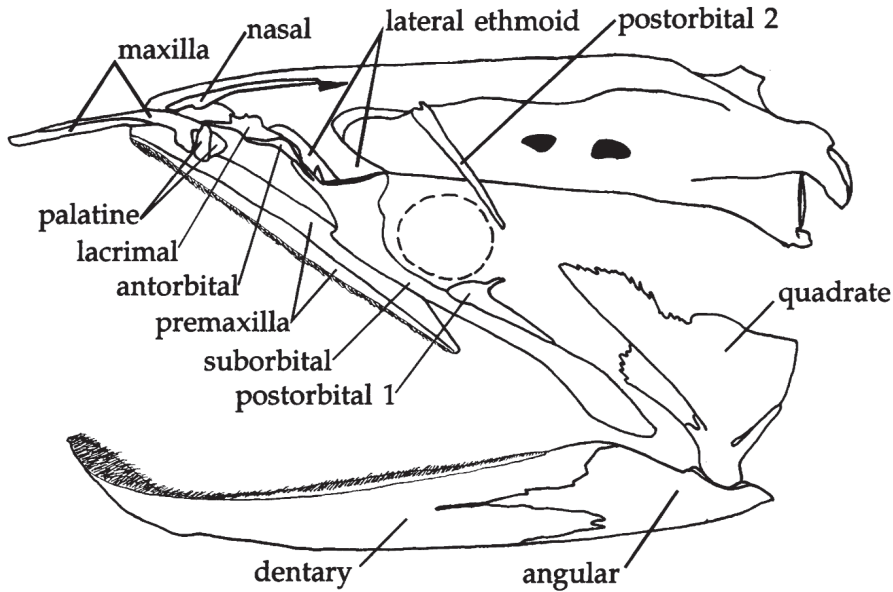
FIGURE 3. *Wallago attu*, lateral view of skull. Pathumtani, Thailand; 960 mm SL.

(Figure 1A); *Wallagonia*—broad and fused together along their entire midline except anteriorly where they form the posterior half of the anterior fontanel; with strong dorsomedian and ventromedian (internal) crests fused into a single crest; posterior fontanel vestigial, represented by a shallow, longitudinal slit on anterior two-thirds of dorsal crest on fused frontal bones (Figure 2A).

SUPRAORBITAL PORTION OF CRANIAL CREST

Wallago—always low (Figures 1B, 3); *Wallagonia*—low in some specimens but in others rising to a high point posterodorsally (apparently not size related, perhaps sex related) (Figures 2B, 4).

ORBITOSPHENOID BONE

Wallago—with a uniformly narrow but very deep trough on its dorsal (i.e., internal) surface ventral to anterior and posterior fontanels (Figure 1A); *Wallagonia*—with narrow and deep trough on its dorsal surface anteriorly but trough closed posteriorly where it underlies vestigial posterior fontanel (Figure 2A).

ORBITONASAL FORAMEN OPENING
ON ROOF OF SKULL

Wallago—by a single large passageway between junction of lateral ethmoid and frontal bones

(Figure 1A); *Wallagonia*—by two large pores on dorsal surface of lateral ethmoid bone; frontal and lateral ethmoid tightly joined with no orbitonasal foramen opening at their junction (Figure 2A).

EPIOTIC BONE

Wallago—with large posteromedian margin of epiotic process deeply indented (or concave), creating an alate or flange-like structure not seen in other silurids (Figure 1); *Wallagonia*—with smaller epiotic process with its posteromedian margin straight or gently convex (as in *Silurus*) (Figure 2).

VENTRAL SURFACE OF BASIOCCIPITAL

Wallago—ventral surface of basioccipital and first vertebral centra with huge condyle-like processes or flanges that overlap broadly and are tightly joined together, the basioccipital condyle external to the vertebral one; *Wallagonia*—ventral surface of basioccipital half centrum and opposing ventral surface of bony enclosure of first vertebral centrum with small, weakly developed processes that do not overlap or interlock and are not strongly attached to each other.

VENTROMEDIAN PREVOMERINE-
PARASPHENOID PROCESS

Wallago—very narrow for its entire length (not tapered anteriorly), its width one-third as great as
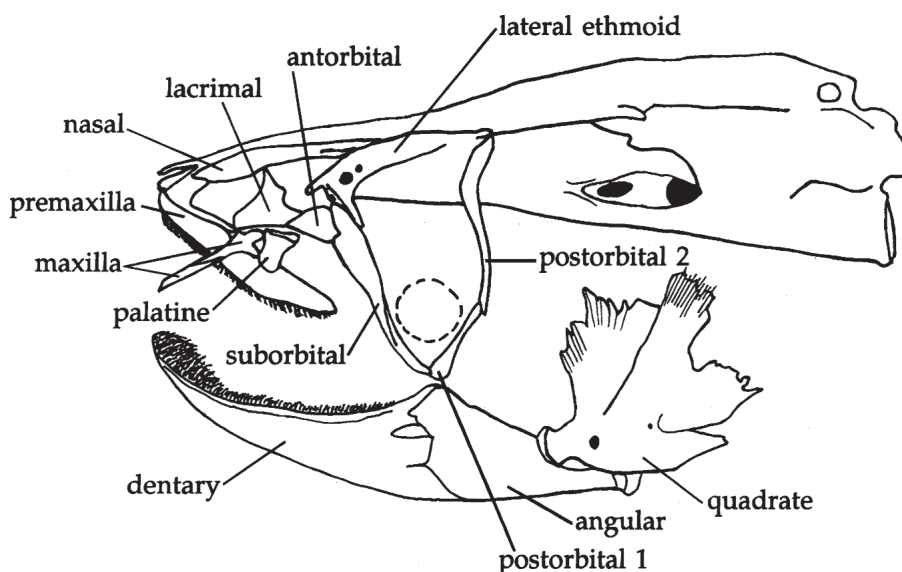
FIGURE 4. *Wallagonia leerii*, lateral view of skull. Palembang, Indonesia; 560 mm SL.

in *Wallagonia* (Figure 1); *Wallagonia*—relatively broad and tapered anteriorly (Figure 2).

QUADRATE BONE VENTRAL SURFACE

Wallago—deeply divided, with a long separate lateral spur or preopercular articular process arising immediately posterior to articular surface with angular bone of lower jaw (Figure 3); *Wallagonia*—with a deep anteroposteriorly oriented oval fossa occupying anterior half of its ventral surface; preopercular articular process arising from posterior border of fossa (as in *Silurus*) (Figure 4).

LATERAL SURFACE OF HYOMANDIBULAR
AND QUADRATE BONES

Wallago—hyomandibular process greatly enlarged (apparently uniquely so in Siluridae), providing greatly expanded surface for attachment of m. levator arcus palatinii; dorsoventral axis insertion of ledge at an angle of about 20° (clockwise) from the vertical (unique to *Wallago*) (Figure 3); *Wallagonia*—with a moderately developed posterodorsally directed ridge or crest as in *Silurus* (hyomandibular process of Kobayakawa 1989, figs. 6, 14); dorsoventral axis of insertion of ledge at an angle of about –45° to –50° (counterclockwise) from the vertical (as in *Silurus* and other silurid genera) (Figure 4).

PECTORAL GIRDLE

Wallago—more elongate; coronoid bone posterolateral to "glenoid fossa" with a short but strong triangular dorsoposterior projection or humeral process; coracoid bone with a narrow medial margin for its entire length; mesocoracoid arch longer, more slender, and strongly curved, creating a large passageway; *Wallagonia*—less elongate; posterior margin of humeral part broadly rounded, without discrete triangular projection; inner margin or coronoid with a deep dorsoventral lamina for most of its length; mesocoracoid arch shorter, stouter, and straight, creating a relatively small passageway.

DORSOMEDIAN BONY LAMINA
OF THE WEBERIAN COMPLEX

Wallago—extends continuously between the skull and the pterygiophores supporting the dorsal fin; *Wallagonia*—continuous between neural spines 3 and 5 but absent between 5 and 6, thus creating a considerable gap in the bony lamina between the skull and the dorsal fin supports (the more usual condition in Siluridae).

Discussion

Several of the characters given above, or the combination of two related ones, would suffice for recognition of the generic distinctness of *Wallago*

and *Wallagonia*. Although the characters given for *Wallagonia* are approached or shared with other silurid and nonsilurid catfish taxa, nearly all of those described in *Wallago* seem to be autapomorphic. Note that the striking occipital condyle described here for *Wallagonia*, although apparently not found in any other Siluridae, is present in several large African and Asian Bagridae (*Bagrus docmak*, *Sperata aor*, *S. seenghala*, *Hemibagrus elongatus*, *H. microphthalmus* and *H. wyckii*), but not in the African bagrid *Bagrus docmak*. The presence of similar condyles in only one (and that highly specialized) species of Siluridae presumably represents independent origin (i.e., parallel evolution) rather than retention of a primitive feature. An alternative hypothesis is that it represents the distant morphological reappearance of an ancient character embedded in the catfish genome.

A much smaller but undoubtedly homologous version of the greatly enlarged "hyomandibular process" or "outer hyomandibular shelf" of *Wallago attu* is present in *Wallagonia* and also in *Silurus*. In all three genera, the ventralmost portion of the shelf is formed by the hyomandibular process of the quadrate bone. This process is much larger in *Wallago* than in *Wallagonia* or *Silurus*.

The difference in overall appearance of the neurocrania of *Wallago* and *Wallagonia* is pronounced. That of *Wallagonia leerii* is wide anteriorly and narrow posteriorly, that of *Wallago attu* the reverse. The cranium of *Wallagonia leerii* is deeply excavated posteriorly to either side of the occipital crest, where the dorsal cranial roof is massively invaded by muscles. That of *Wallago attu*, with a minimal crest, is hardly depressed or excavated and has little muscle attachment.

Wallagonia, like *Silurus* and other silurid genera, has a connected or continuous system of bony troughs (more or less partially open toward the surface) and canals for passage of the circumorbital branch of the cephalic laterosensory canal system. This is facilitated by the near contact or overlap of the distal and proximal ends of the successive bones in the circumorbital series. Most of these consist mainly of the trough-like or tubular component, with little or no laminar component. The condition in *Wallago* is quite different, mainly because of the extreme modification of the greatly enlarged suborbital and of the much smaller first postorbital. The other elements in the series—the lacrimal, antorbital and second (last) postorbital—retain their trough-like or canal-like passageways for the circumorbital laterosensory canal. However, I find no trough-like structure or canal in the suborbital and first postorbital bones of *Wallago*. There is no opening or pore for entry or exit of the membranous laterosensory canal at either end of these bones or in the middle of the suborbital bone where the anterior and posterior ends of the first postorbital lie. Presumably the laterosensory canal passes along the surface of these bones without entering them. There is between the posterior end of the first postorbital and the lower end of the second postorbital a considerable gap that must be crossed by the lateral line canal where it is not closely associated with any bone.

The surface area of the dentigerous portion of the jaws (i.e., that part occupied by tooth sockets) in *Wallagonia leerii* is 58% to 64% of that in *Wallago attu*. Because the teeth of *Wallagonia leerii* are also much smaller than those of *Wallago attu*, the functional surface area of the jaw teeth of the latter is more than twice that of the former. The gape, difficult to measure accurately in dried skeletal preparations, presumably is proportionately greater in *Wallago attu*. The snout-to-vent distance is also nearly twice as great in *Wallago attu* as in *Wallagonia leerii*. The foregoing means that *Wallago attu* probably can swallow a prey fish twice as large as *Wallagonia leerii* of the same size. Note that *Wallagonia leerii* probably grows at least twice as large as *Wallago attu*. The largest *Wallago attu* are only about 1 m long. *Wallagonia leerii* get much bigger. Fishermen brought a fish over 2 m long and said to weigh 95 kg to Stung Treng, on the Mekong River in northeast Cambodia, while I was there. Both species probably feed predominantly on cyprinids. Maximum size attained by large *Wallago attu* and *Wallagonia leerii* may be correlated with the larger size of cyprinid prey species that they are likely to encounter. A 1 m *Wallago attu* presumably can swallow a fish as large as can a 2 m long *Wallagonia leerii*.

Osteological material of *Wallago attu* has been relatively available for a long time, that of *Wallagonia leerii* much less so. *Wallagonia leerii* is perhaps most closely related to *Ompok* (Bornbusch 1995; pers. obs.), and not at all closely related to *Wallago attu*. While I have not exam-

FIGURE 5. Type locality of *Wallago maemohensis* at Mae Moh Coal Mine in northwestern Thailand.

ined osteological preparations of *Ompok*, I have examined many specimens of that genus, including the morphologically generalized *Ompok bimaculatus* (Bloch, 1794) and the type species of the genus, *O. siluroides* Lacepède, 1803. These are much more similar morphologically (and therefore presumably also osteologically) to *Wallagonia* than to *Wallago*. *Wallago* and *Wallagonia* do not seem to be closely related to each other. *Wallago* dates back at least to the Miocene (and probably much earlier). Relationships of *Wallago* (*sensu stricto*) to other silurid taxa have not been properly studied. I doubt that *Wallago* and *Wallagonia* are close relatives, but am unable to identify a particularly close relative of *Wallago*.

Consideration of their geographical distributions or ranges also suggests that *Wallago* could be the older of the two genera. *Wallagonia* has what may be a relatively youthful (and perhaps still expanding) distribution. It is restricted geo-graphically to a relatively small but contiguous or continuous range in Southeast Asia, including the Meklong, Chao Phraya, and Mekong, Malay peninsula, central and southeast Sumatra, and Borneo (including northeast, eastern and southeast Borneo). Its absence from Java is noteworthy.

Wallago, on the other hand, has a much greater and possibly older distribution with significant disjunctions or gaps (d'Aubenton and Blanc 1967:286, fig. 3; Roberts 1982). It occurs in two main geographical areas, one in mainland Asia and the other in Indonesia. One area is on the mainland, where it occurs in the Indus basin and the Ganges and its tributaries in India and Bangladesh, and in the Irrawadi basin in Myanmar. It either does not occur in the Salween or Tenasserim River basins or is not well documented from them. It then occurs in the Meklong, Chao Phraya and Mekong, and in the Malay Peninsula, Sumatra and Java. It apparently is

FIGURE 6. *Wallago maemohensis*, cranium, 104 mm long with left premaxillary bone (holotype). **A,** Part, ventral view (without cleaning). **B,** Counterpart, ventral view (without cleaning).

absent from Borneo, surprisingly so, because it is present in Sumatra and Java. This suggests that it formerly occurred in Borneo but was extirpated from there. There was no published fossil record for either *Wallago* or *Wallagonia* until now.

Of the species referred to *Wallago* by recent workers, only *Wallago attu* (Bloch and Schneider, 1801), with *Silurus muelleri* Bleeker, 1846 as a junior synonym, is referable to *Wallago* as here understood. *Wallagonia* includes *Wallagonia leerii* Bleeker, 1851, *Wallagonia maculatus* Inger and Chin, 1959 (known from northeastern Borneo, possibly synonymous with *W. leerii*), and the recently described and scarcely distinct *Wallagonia micropogon* Ng, 2004, described from the Mekong and Chao Phraya basins (also possibly synonymous with *W. leerii*). *Wallagonia leerii* and *Wallagonia micropogon* seem to be osteologically indistinguishable. Osteological observations attributed here to *W. leerii* apply equally to *W. micropogon*.

Species Description

†*Wallago maemohensis* Roberts, new species
Figures 5–7, Table 1

Type material. *Holotype.* Thailand Department of Mineral Resources (Bangkok), catalog of fossil vertebrates no. 7664, complete neurocranium with left premaxilla, length of neurocranium 104 mm, 30 August 1998, Tyson R. Roberts.

Locality and horizon. Mae Moh coal mine about 30 km SE of Lampang, near center of NW mining pit area, Lampang province, northern Thailand (Figure 5). The Mae Moh vertebrate deposits including the fish reported here are now thought to be of mid-Miocene age, ca. 12–13 my. Evidence for this age comes from correspondence of mammalian (Tassy et al. 1992) and molluscan (Songtham et al. 2005) species from other sites that are relatively well dated and from magnetostratigraphic studies (Bennammi et al. 2002).

Diagnosis. An extinct species of *Wallago* probably attaining 1 m or more in length, distinguished from all other silurid genera by its extremely large premaxillary bone and distinctively shaped cranium, especially the lateral ethmoid with a double articular surface and the epiotic bone with a concave medioposterior margin. Width of the skull across the sphenotic bones, 41.3%, is notably more than in living *Wallago* (Table 1).

Description. The holotype is a complete neurocranium, 104 mm total length, with the complete left premaxillary still bearing many teeth. The jaws otherwise are entirely lacking. At first glance the skull appears to be in perfect condition, such that one could seemingly disarticulate it and study the morphology of the individual skull bones. Unfortunately this is not the case. *Wallago* has extraordinarily numerous, long, delicate spicule-like osseous interdigitations between skull bones. When the skull was fossilized, these were crushed. Despite this difficulty it is clear that the skull is that of a *Wallago* and not that of a *Wallagonia*. Thus hypotheses advanced here about the *Wallago*-like morphology of bones that have been lost from the fossil, such as the suborbital, have a fairly strong basis. Part and counterpart (or slab and counterslab) of the specimen, separated by the author in the field in the act of collecting the specimen, show the ventral surface of the neurocranium and left premaxillary with numerous teeth and deep tooth sockets where teeth are missing (Figure 6A, B). The dorsal surface of the part was later cleaned in Paris (Figure 7A) and the neurocranium radiographed (Figure 7B).

Observations. The overall conformation of the neurocranium and premaxillary readily permit identification of the fossil as a *Wallago* (compare Figures 6 and 7 with Figure 1A and 1C). The left premaxillary bone of the fossil is approached in size and length among living silurids only by that of *Wallago attu*, in which the mode of attachment of the premaxillary is highly specialized and apparently unique (see above). The mode of attachment of the premaxillary to the skull is unknown in the fossil but presumably it was like that in living *Wallago*. This seems likely

because of the reduced width of the ethmoid bone and the biccipital morphology of the distal end of the lateral ethmoid bone in the fossil. Whether the fossil had the same sort of highly specialized suborbital 3 as in living *Wallago* is unknown. There is no sign of this feature in the fossil. It also unclear whether *W. maemohensis* has the highly specialized basioccipital-atlas centrum morphology diagnostic of living *Wallago* (Tilak 1961). The basioccipital centrum has a pair of large, ventral, posteriorly directed condyles that articulate with similar but smaller anteriorly directed processes arising on the atlas vertebrae. In *Wallago* the anterior end of the atlas centrum is convex, rather than concave as in all other silurids. In these respects the condition in *W. maemohensis* is unclear. The shape of the lateral ethmoid of the fossil approaches that of the highly specialized lateral ethmoid of *Wallago*. The skull shape also is generally similar to that of living *Wallago* except that it is somewhat less elongate. In other words, the dorsoventral outline of the fossil skull is more nearly rectangular. This is reflected in its relatively greater sphenotic width, 41.3% of cranial length as compared with only 31.5% to 33.7% in modern *Wallago attu* (Table 1).

As in all silurids except *Belodontichthys*, the fossil *Wallago* has elongate teeth with very sharp tips. If these tips may appropriately be termed "needle-like," *W. maemohensis* has the most needle-like jaw premaxillary teeth of any known silurid, even more so than *Wallago attu*. *Belodontichthys* teeth have arrow-shaped tips (Figure 8).

In the fossilized cranium of *Wallago maemohensis*, the premaxillary bone extends laterally from the ethmoid region at the anterior end of the skull in a way that is not observed in living *Wallago* species. This presumably is an artifact. In living species of *Wallago* the premaxillary is attached to the side of the skull by way of the enlarged and otherwise modified third suborbital bone. In silurids other than *Wallago*, almost the entire premaxillary bone is attached to the ventral surface of the mesethmoid. If the lateral position of the premaxillary seen in the fossil was normal, one would expect it to have a laterally expanded mesethmoid. The mesethmoid in the fossil, however, is narrow as in living *Wallago*.

C. Tate Regan, in 1911, distinguished Siluridae from all other catfish families as having the frontal bones excluded from the cranial margin by the lateral ethmoid and sphenotic bones (Regan 1911). This character was accepted as a silurid synapomorphy by Bornbusch (1995). Note that the frontal bones are thus excluded from the cranial margin in several species of *Silurus*, but not in others (Kobayakawa 1989, e.g., *Silurus grahami*, fig. 19a; *S. mento*, fig. 22a, b; *S. torrentis*, fig. 34a, b). The frontals are excluded in *Wallago* and *Wallagonia*. It is difficult to be sure of the condition in the cranium of *Wallago maemohensis*, but here also it seems likely that the posterior extensions of the lateral ethmoids and the anterior extensions of the sphenotics do meet and that the frontal bones are thus excluded.

The silurid catfish genus *Wallago* occurs in two main geographical areas, one in mainland Asia and the other in Indonesia (d'Aubenton and Blanc 1967:286, fig. 3; Roberts 1982). On the mainland it occurs in the Indus basin and the Ganges and its tributaries in India and Bangladesh; in the Irrawadi River in Myanmar; in the Meklong, Chao Phraya and Mekong basins; and in the Malay peninsula. In Indonesia it occurs only on Sumatra and Java.

Whereas *Wallagonia* is continuously distributed within its relatively restricted range, *Wallago* has two or perhaps three
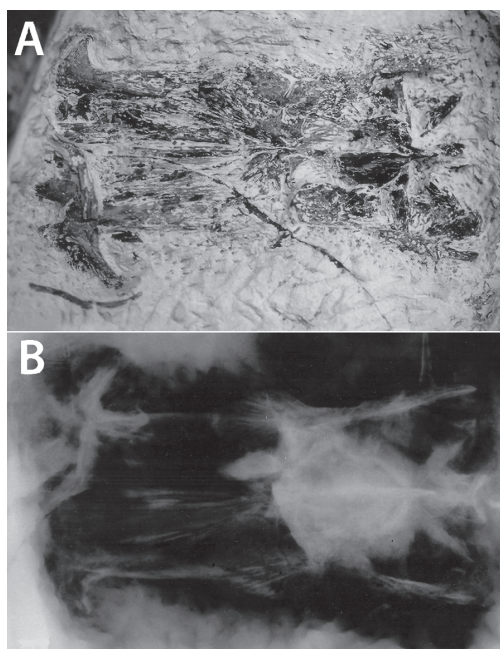
FIGURE 7. *Wallago maemohensis*, cranium, 104 mm long. **A,** Part, dorsal view of cranium (extensively cleaned). **B,** Radiograph.

TABLE 1. Cranial measurements of *Wallago maemohensis* holotype and three *Wallago attu* specimens from the Mekong basin in Cambodia. Proportional measurements are given as a percentage of cranial length.

Character	*Wallago maemohensis*	*Wallago attu*
Cranial length (mm)	104	102–175
Ethmoid width	—	27.7–29.5
Lateral ethmoid width	52.9	48.8–52.6
Sphenotic width	41.3	31.5–33.7
Pterotic width	40.4	39.2–41.0
Premaxillary length	57.7	56.4–57.1
Mandibular length	—	89.5–95.0

major disjunctions in its range, an indication that it could be a much older taxon. It apparently is absent from the Salween and Tenasserim (or Tananthayi) rivers, and is also absent from Borneo. As treated by recent workers, *Wallago* includes only a single species, *Wallago attu* Bloch and Schneider, 1801, with *Silurus muelleri* Bleeker, 1846 as a junior synonym. There is no previous fossil record for *Wallago*.

The catfish genus *Wallago* (with *Wallagonia* excluded) generally is regarded as containing a single widely distributed species, with populations in the Indus, Ganges, South India, Sri Lanka, Myanmar, Thailand and Indo-China, the Malay Penin-
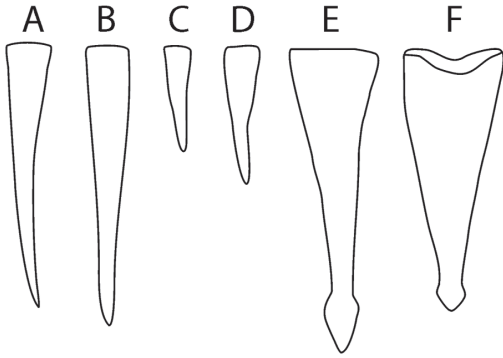
FIGURE 8. Silurid premaxillary teeth. **A,** *Wallago maemohensis*. **B,** *Wallago attu*. **C,** *Wallagonia leerii*. **D,** *Silurus glanis*. **E,** *Micronema* sp. **F,** *Belodontichthys dinema*. **G,** *B. truncatus*. Teeth drawn to same scale using 104 mm cranial length of holotype of *Wallago maemohensis* as standard.

sula, Sumatra, and Java. The single species concept may not be valid. Bone-by-bone comparison of the skulls of *Wallago attu* (type locality Malabar) from South India and *Wallago* from the Mekong basin indicates that they are not conspecific. Hence it is likely that *Wallago muelleri* (type locality Java) is a valid species. Comparative material from Java is not available, so I am unable to define this nominal species or to compare it with other *Wallago*, including the fossil *W. maemohensis*.

Acknowledgments

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