

Spiny eels of the genus *Mastacembelus* in the Mekong drainage in Laos, with description of *M. dictyon* (Teleostei: Synbranchiformes)

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Abstract. *Mastacembelus dictyon*, new species, a spiny eel of the *M. armatus* species group, is described from the Mekong drainage in Laos. It is distinguished from *M. armatus* by having fewer caudal-fin rays (13–15 vs 18–20), fewer abdominal (35–39 vs 42–43), caudal (47–51 vs 51–55), and total vertebrae (85–90 vs 94–97), and by fewer dorsal-fin spines (33–37 vs 37–38); and from *M. favus* by differences in colour pattern. Earlier records of *M. favus* from Laos are not confirmed, but its presence there is possible; a lectotype is designated for *M. favus*. A neotype is designated for *M. armatus*; its type locality is in the Ganges drainage, India. Previous neotype designations for *M. undulatus* and *M. thacbaensis* are invalid. A neotype is designated for *M. undulatus*, making it an objective junior synonym of *M. armatus*. The presence in Laos of *M. dienbienensis*, *M. thacbaensis*, and *M. tinwini* is confirmed.

Key words. Mastacembelidae, *Mastacembelus armatus* group, Mekong basin, lectotype, neotype

INTRODUCTION

The Asian spiny eels *Mastacembelus armatus*, *M. favus*, *M. tinwini*, *M. pantherinus*, and *M. undulatus* form a complex of putatively closely related species: the *M. armatus* group (Britz, 2007). They attain large sizes of over 50 cm and are food fishes that are frequently encountered in local markets (Sufi, 1956; Roberts, 1986; Kottelat, 2001a; Britz, 2007). In addition to their large size, species of the *M. armatus* group are characterised by a pattern of undulating dark colour markings on the body arranged in series of horizontal lines, sometimes broken up into blotches, and series of shorter vertical markings interconnecting the horizontal lines (see below for terminology).

Sufi (1956) was the last author to examine material from a large area of the distribution range of *M. armatus*, which he considered to extend from Pakistan eastwards to southern China and southwards to the Sunda Islands. Although Sufi (1956) cited obvious differences in colour pattern, as well as unusually large ranges for the number of fin rays and vertebrae among the populations of *M. armatus*, he synonymised several nominal species under this name.

In a revision of the mastacembelids from Thailand and Myanmar, Roberts (1986) removed *M. favus* from the

synonymy of *M. armatus* and provided information to distinguish the two species. He reported the presence of the two species in the Mekong drainage (Thailand). Studying the spiny eels of the *M. armatus* group from throughout Myanmar, Britz (2007) described two additional species, *M. tinwini* from the Sittaung and Salween drainages and *M. pantherinus* from Lake Indawgyi, and provided additional information on the species of the *M. armatus* group from Myanmar.

Since Roberts (1986), there have been a number of reports of *M. armatus* from the Mekong drainage (e.g., Rainboth, 1996; Rainboth et al., 2012; Kottelat, 1998, 2001a, 2011, 2016; Baird et al., 1999; Vidthayanon, 2008; Praxaysombath et al., 2020). Kottelat (1998: 17) speculated that the Mekong *M. armatus* “could represent an unnamed species”. A detailed comparison between the spiny eels referred to as *M. armatus* from the Mekong and *M. armatus* from India and Myanmar revealed consistent differences in vertebral counts and colour pattern between the two, and demonstrated that the Mekong *M. armatus* is an unnamed species for which we make a name available in this paper. In recent years, others have reported the existence of two additional species in the Mekong drainage in Laos and Thailand, which they identified as *M. cf. pantherinus* and *M. cf. tinwini* (e.g., Praxaysombath et al., 2020: 115; Nagao Natural Environment Foundation, 2021: 351).

MATERIAL AND METHODS

Measurements were taken with digital callipers to the nearest 0.1 mm from specimens larger than 100 mm standard length (SL). Standard length is given to the nearest 0.1 mm for specimens smaller than 100 mm SL, to the nearest mm

Accepted by: Kevin W. Conway

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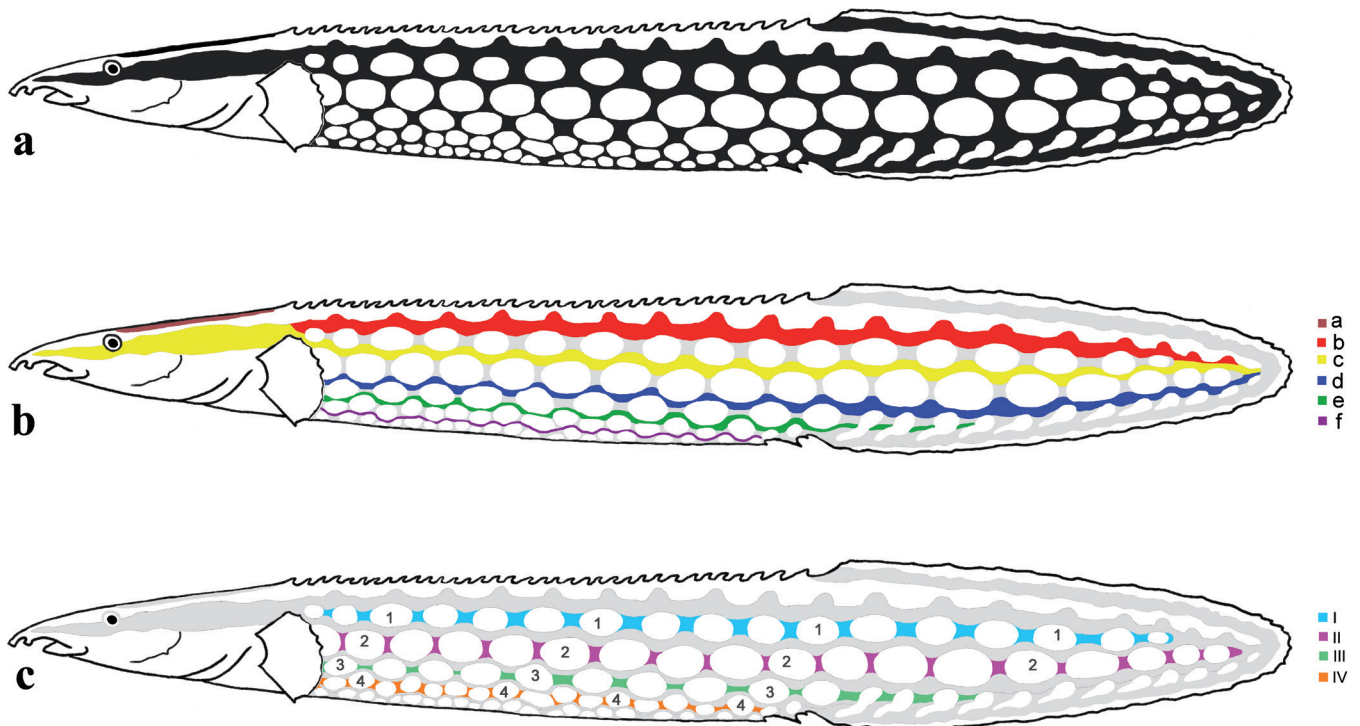


Fig. 1. Terminology of stripes, bars and blotches in the *Mastacembelus armatus* group. a, Schematic drawing of hypothetical complete set of dark markings. b, Stripes a–f colour-coded, as on legend on image: stripe a, brown; stripe b, red; stripe c, yellow; stripe d, blue; stripe e, green; stripe f, purple. c, Bars of series I–IV colour-coded, as on legend on image: bar series I, sky blue; bar series II, pink; bar series III, light green; bar series IV, orange. Blotch series 1–4 marked with respective numbers. Irregular dark markings, shown in gray, cover abdominal region ventral to bar series IV.

for specimens larger than 100 mm SL. For measurements, the anteriormost point on the snout is found by bending the proboscis ventrally and pushing the calliper against the snout finding a firm point, which is more or less equal to the anteriormost tip of the mesethmoid. In general, obtaining accurate measurements in mastacembelids may prove difficult because specimens are frequently preserved in a bent or twisted state. Usage of the terms fimbriae and fimbriules follows Travers (1984).

Vertebral numbers were counted from radiographs. Fin-ray counts for unpaired fins were also obtained from radiographs, those of pectoral fins from alcohol-preserved specimens under transmitted light; counting the number of pectoral-fin rays may present difficulties especially with regard to the small rays at the margins of the fin, which could easily be overlooked. A number of specimens of the different samples we examined show teratological aberrations or malformations that make them unsuitable for a detailed analysis. One kind of malformation was in the caudal area, which often showed signs of regeneration, either of just the caudal fin and its supporting skeleton, or of several caudal vertebrae as well. Frequently vertebral elements showed teratological anomalies with double or even more numerous neural and/or haemal spines. Specimens exhibiting such damage, regeneration, or signs of teratological anomalies were excluded from the analysis of meristic and morphometric data.

The terminology (Fig. 1) for the colour pattern of species from the *M. armatus* group is adapted from Sufi (1956) and Britz (2007), in which the dark longitudinal markings

(their “bands”) on the body are labeled with letters a–f. Deviating slightly from their terminology, we use ‘stripe’ for longitudinal dark markings, rather than ‘band’ to follow standard practice in ichthyology. Stripe terminology is as explained in the following paragraphs and illustrated in Fig. 1. **Stripe a**, not well expressed in *Mastacembelus dictyon*, is the mid-dorsal dark marking from snout to nape or sometimes to the anterior dorsal-fin spine. Stripe a may be broken up into several shorter stripes or blotches. Stripe b is the dorsalmost marking that runs along the back just below the dorsal-fin spines, starting above the base of the pectoral fin, sometimes running posteriorly as far as the end of the dorsal fin or stopping before this. **Stripe b** is often broken up into a series of short stripes or round blotches. **Stripe c** is the straight or slightly undulating stripe on the dorsal half of the body, running in close proximity to the lateral-line canal, from the tip of the snout to the caudal-fin base. Stripe b may merge with stripe c above the pectoral fin. **Stripe d** is the straight or slightly undulating stripe running from the middle of the base of the pectoral fin towards the middle of the anal fin, ending at the caudal-fin base. **Stripe e** is the straight or undulating stripe running from the ventral extremity of the base of the pectoral fin towards the anterior base of the anal fin. There is sometimes an additional incomplete and irregular **stripe f**, which runs along the lateroventral side of the belly towards the anterior base of the anal fin. In some specimens of *M. dictyon* and generally in *M. favus*, the ventrolateral and ventral abdominal region is covered by an irregular network of dark markings that cannot be grouped into stripes or bars.



Fig. 2. *Mastacembelus dictyon*, holotype, MHNG 2804.002, 170 mm SL; Laos: Mekong drainage: Nam Ngiep watershed. a, preserved; b, 6 weeks after fixation.

Stripes b, c, d, and sometimes e, are connected to the stripe immediately below (b connected to c, c to d, d to e, e to f) by series of vertical marks, here called bars and numbered with upper case Roman numerals, so that **bar series I** connects stripes b and c, **bar series II** connects stripes c and d, **bar series III** connects stripes d and e, and **bar series IV** connects stripes e and f.

The light blotches that are separated by these interconnecting stripes and bars are arranged as parallel series, as follows: **blotches of series 1**, bordered dorsally by stripe b, ventrally by stripe c and separated from each other in the series by interconnecting bar series I; **blotches of series 2**, bordered dorsally by stripe c, ventrally by stripe d and separated by interconnecting bar series II; **blotches of series 3**, bordered dorsally by stripe d, ventrally by stripe e and separated by interconnecting bar series III; **blotches of series 4**, bordered dorsally by stripe e, ventrally by stripe f and separated by interconnecting bar series IV.

Toponymy follows the official maps of Laos (Service Géographique d'Etat, 1:100,000 series, 1985–1987) and Thailand (Royal Thai Survey Department, 1:250,000 series, 1975–1988). *Code*: International Code of Zoological Nomenclature. Code of collections mentioned in the text: ANSP: Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, U.S.A.; BMNH: The Natural History Museum, London, U.K.; CMK: Personal collection of Maurice Kottelat, Delémont, Switzerland; MHNG: Muséum d'Histoire Naturelle, Genève, Switzerland; MNHN: Muséum National d'Histoire Naturelle, Systématique et Évolution, Laboratoire d'Ichtyologie Générale et Appliquée, Paris, France; MTD: Senckenberg Naturhistorische Sammlungen Dresden, Germany; NRM: Naturhistoriska Riksmuseet, Stockholm, Sweden; RMNH: Naturalis - Nationaal Natuurhistorisch Museum, Leiden, the Netherlands; SMF: Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany; ZMB: Museum für Naturkunde, Berlin, Germany; and ZSI: Zoological Survey of India, Kolkata, India.

***Mastacembelus dictyon*, new species**
(Figs. 2, 3a, 4a, 7–12)

Holotype. MHNG 2804.002, 170 mm SL; Laos: Saysomboune Province: Thathom District: Nam Ngiep watershed: Nam Khai, about 1.5 km upstream of confluence with Houay Hok; 341 masl; 18°56'03"N 103°26'40"E; M. Kottelat et al., 11 March 2018.

Paratypes. Laos: Mekong drainage: NAM NGUM WATERSHED: CMK 13400, 3; Vientiane Prov.: Nam San downstream of Ban Pa Man, tributary of Nam Ngum reservoir; 18°32'03"N 102°55'48"E. — CMK 22427, 1; Vientiane Prov.: Nam Ngum at bridge on road to site of Nam Ngum 3 powerhouse; 18°59'28"N 102°50'21"E. — CMK 23823, 5; Vientiane Prov.: Nam San rapids near km-mark 54 on road from Thabok to Phubia mine, about 8 km south of Ban Xieng Mi, 10 km north of Ban Longxan; 18°35'42"N 103°04'41"E.

Laos: Mekong drainage: NAM NGIEP WATERSHED: CMK 24333, 2; Saysomboune Prov.: Houay San, immediately upstream of confluence with Nam Ngiep, 23 km downstream of Ban Pou, 18 km upstream of Ban Soppouan, 18°53'11"N 103°28'07"E. — CMK 24362, 1; Saysomboune Prov.: Houay Hok, a small creek entering Nam Ngiep, 3.5 km south of Ban Soppouan on road to Ban Sopyouak; 18°44'57"N 103°25'28"E. — CMK 24665, 1; Saysomboune Prov.: Nam Sao, tributary of Nam Ngiep, entering it about 1 km downstream of Ban Sopyouak; 18°43'38"N 103°28'14"E. — CMK 24685, 3; Bolikhamsai Prov.: Nam Xao upstream of bridge on road from Ban Muanghuang to Ban Nahan; 18°45'33"N 103°32'57"E. — CMK 24712, 8; Bolikhamsai Prov.: Nam Xao, Hart [Keng] Sarng Pa Fa, 2.5 km upstream of Ban Thahua; 18°40'13"N 103°37'26"E. — CMK 27524, 1; Saysomboune Prov.: Houay Hok upstream of confluence with Nam Khai; 18°55'13"N 103°27'16"E. — CMK 27544, 1; same data as holotype. — CMK 27625, 2; Saysomboune Prov.: Nam Thaeng (tributary of Nam Ngiep, entering at Vieng Thong) at Ban San Phou Xay, about 5 km from confluence with Nam Ngiep; 19°03'17"N 103°19'14"E. — CMK 27665, 4; Saysomboune Prov.: Thathom: Nam Long, about 150 m upstream of confluence with Nam Chae; 19°02'07"N 103°30'00"E. — CMK 27758, 1; Saysomboune

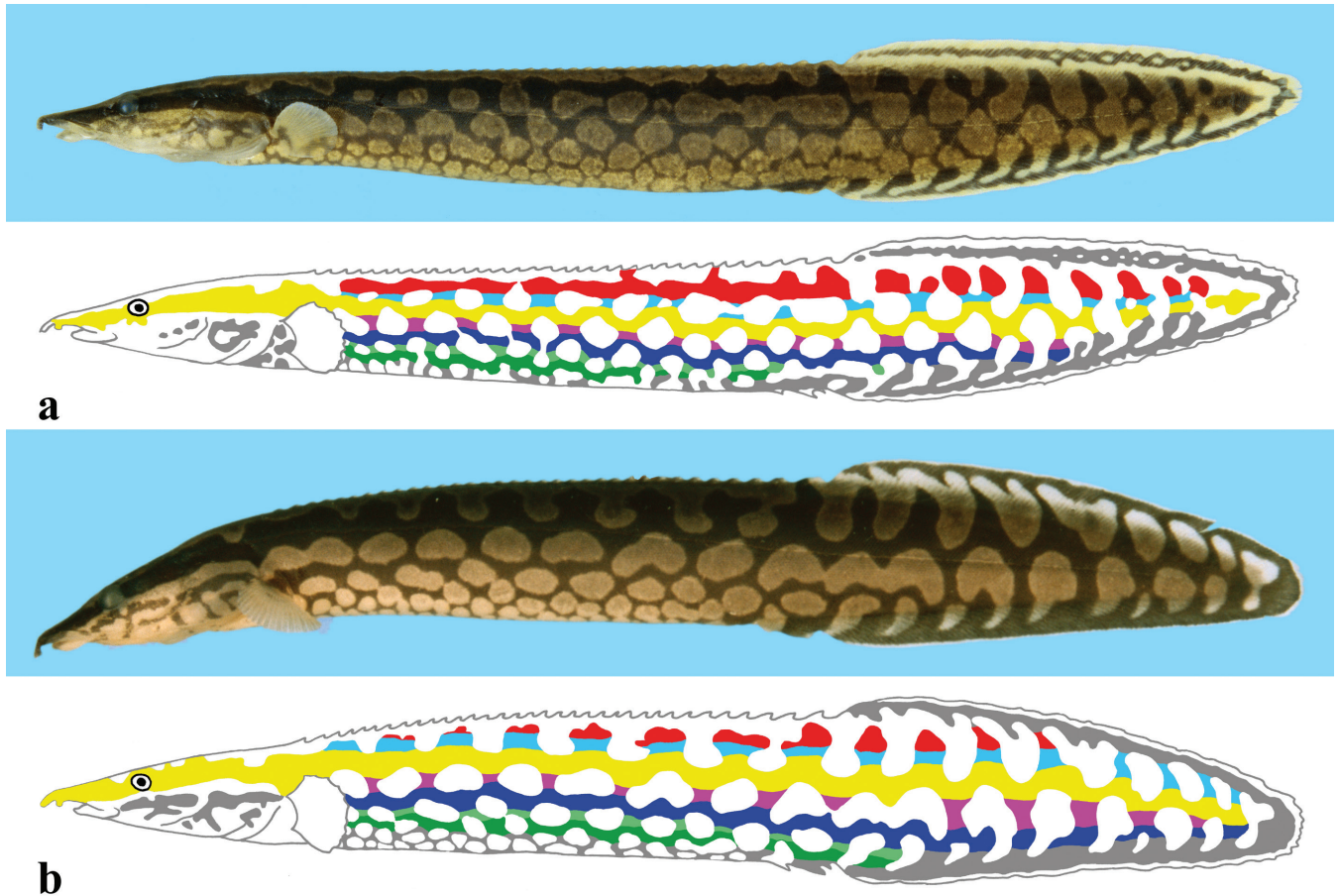


Fig. 3. a, *Mastacembelus dictyon*, CMK 12786, 146 mm; Laos: Mekong drainage: Nam Kading watershed: Nam Theun; actual specimen and schematic drawing with coloured coded dark markings. b, *M. favus*, CMK 20188, 126 mm; Thailand: Chantaburi Province: Mekong drainage: Tonle Sap watershed; actual specimen and schematic drawing with colour coded dark markings. Stripe a not shown. Note presence of stripe b (red) in *M. dictyon* and its reduction to blotches in *M. favus*. For explanation of colour coding, see Fig. 1.

Prov., tributary of Houay Hok, itself a tributary of Nam Ngiep, entering it about 100 m from mouth; 18°56'28"N 103°29'54"E. — CMK 27939, 1; Saysomboune Prov.: Houay Hok, tributary of Nam Ngiep, 400 m upstream of confluence; 18°56'26"N 103°30'02"E. — CMK 29128, 1; Saysomboune Prov.: Houay Tom, stream entering Nam Ngiep reservoir, about 200 m from reservoir; 18°42'02"N 103°22'58"E.

Laos: Mekong drainage: NAM XAN WATERSHED: CMK 24621, 4; Bolikhamxai Prov.: Borikhan: Nam Xan downstream of Ban Pakhuang; 18°40'58"N 103°47'09"E.

Laos: Mekong drainage: NAM KADING WATERSHED (including Nam Theun): CMK 12509, 13; Bolikhamxai Prov.: rapids on Nam Gnouang downriver of Ban Thabak; 18°16'50"N 104°38'00"E. — CMK 12512, 1; Khammouan Prov.: Nam Theun, rapids about 17 km upriver of Ban Thabak bridge; 18°10'35"N 104°44'44"E. — CMK 12786, 6; Khammouan Prov.: Nam Theun at confluence with Nam Phao; 18°02'51"N 104°57'18"E. — CMK 18139, 12; Khammouan Prov.: side arm of Nam Xot, upstream of Keng Luang; 17°57'05"N 105°08'18"E. — CMK 19252, 12; Khammouan Prov.: upper Nam Theun, rocky outcrop; 17°48'53"N 105°20'37"E. — CMK 22881, 12; Khammouan Prov.: upper Nam Theun at Keng Heng rapids, downstream of Ban Sok Lek; 17°55'12"N 105°22'56"E.

Additional material (not types). Laos: Mekong drainage: NAM YOUAN WATERSHED: CMK 25967, 2; Louang Namtha Prov.: Muang Sing: Nam Youan at Ban Mom; 21°19'32"N 101°10'28"E.

Laos: Mekong drainage: NAM MA WATERSHED: CMK 25950, 1; Louang Namtha Prov.: Muang Long: Nam Ma Oun, a branch of Nam Ma, downstream of Ban Phang Thong; 21°04'55"N 101°03'37"E. — CMK 26057, 1; Louang Namtha Prov.: Muang Long: confluence of Nam Ma and Nam Long at Muang Long; 20°58'03"N 100°49'08"E.

Laos: Mekong drainage: NAM OU WATERSHED: CMK 21028, 7; Phongsali Prov.: Muang Mai: Nam Noua at Keng Pan, upstream of Ban Bouamphan; 21°13'48"N 102°49'29"E. — CMK 29198, 1, 208 mm SL; Phongsali Prov.: Muang Gnot Ou: Nam Ou, downstream of Gnot Ou, Haat Veune rapids; 22°05'02"N 101°46'51"E. Additional material: 4 specimens from 2 sites.

Laos: Mekong drainage: NAM HEUNG WATERSHED: CMK 28063, 1; Xayaburi Prov.: Boten Distr.: Nam Hoy, Keng Thiane rapids, 8 km south of Nakok on road to Ban Boten; 17°42'15"N 101°10'43"E. — CMK 28082, 2; Xayaburi Prov.: Kemethao Distr.: Nam Heung, rapids Keng Ban Veun at Ban Mouang Mor, 7 km South of Kenethao; 17°40'59"N

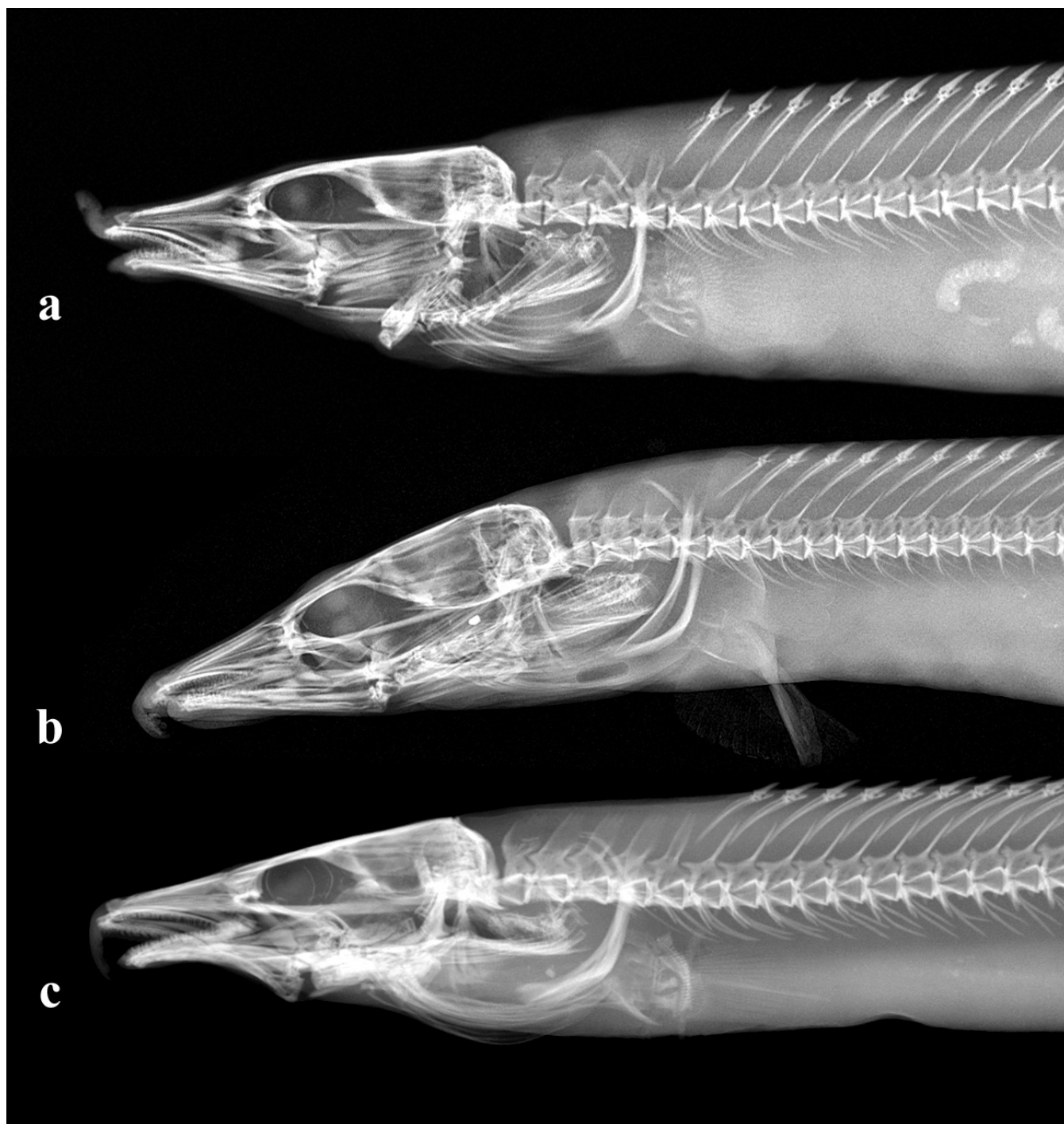


Fig. 4. Radiographs of: a, *Mastacembelus dictyon*, MHNG 2804.002, holotype, 170 mm SL; b, *M. favus*, CMK 20188, 126 mm SL; and c, *M. thacbaensis*, ANSP 210057, 216 mm SL. Note anterior insertion of first dorsal-fin spine behind 4th neural spine in *M. dictyon* and *M. favus* and behind 5th neural spine in *M. thacbaensis*.

101°24'03"E. Additional material: 1 specimens from 1 site in Thailand.

Laos: Mekong drainage: NAM NGUM WATERSHED: CMK 23784, 1; Houay Gniou, tributary of Nam San, at Ban Xiangmi, road from Ban Longxan to Ban Namcha; 18°40'29"N 103°06'28"E. Additional material: 4 specimens from 2 sites.

Laos: Mekong drainage: NAM MANG WATERSHED: CMK 13320, 2; Vientiane Prov.: Nam Leuk at dam site; 18°26'15"N 102°56'48"E. — CMK 24427, 6; Saysomboune Prov.: Khon:

Nam Mang near Ban Pa La Veak; 18°40'01"N 103°12'06"E. Additional material: 4 specimens from 3 sites.

Laos: Mekong drainage: NAM KADING WATERSHED (including Nam Theun): additional material: 172 specimens from 46 sites.

Laos: Mekong drainage: XE BANGFAI WATERSHED: — CMK 12277, 3; Khammouan Prov.: Xe Bangfai, about 1 km upstream of confluence with (unnamed) stream descending from Phou Taloun; 17°09'42"N 106°12'33"E. — CMK 12363,



Fig. 5. *Mastacembelus pantherinus*, CMK 24226, 212 mm SL; Myanmar: Lake Indawgyi (reversed).

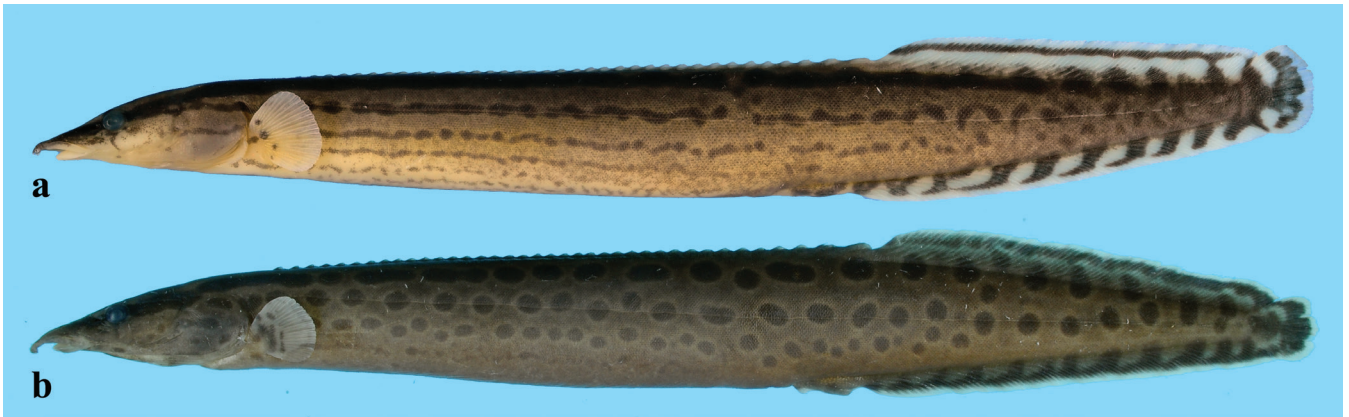


Fig. 6. *Mastacembelus tinwini*, a, CMK 27468, 105 mm SL; Myanmar: Sittaung; b, CMK 24947, 146 mm SL; Myanmar: Tenasserim.

9; Xe Bangfai, ford 1 km upriver of mouth of Nam Oula; 17°22'59"N 105°11'46"E. — CMK 12618, 3; Khammouan Prov.: Xe Bangfai about 3 km upriver of Ban Pakphanang; 17°24'20"N 105°45'50"E. — CMK 17176, 1; Khammouan Prov.: Xe Bangfai, between Ban Pakphanang and about 2 km upriver; 17°24'00"N 105°43'55"E. — CMK 19064, 11; Khammouan Prov.: Xe Bangfai at Keng Padek, about 1.5 km downstream of confluence with Nam Phit; 17°20'42"N 105°12'35"E. — CMK 19272, 10; Khammouan Prov.: Xe Bangfai about 2 km upstream of Ban Pon Keo; 17°29'30"N 105°26'21"E. — CMK 23100, 30; Savannakhet Prov.: Xaybouli District: Xe Noy at Keng Boua upstream of Ban Dongmarfai, 6 km on road east, then 1 km on track north; 17°04'21"N 105°03'27"E. Additional material: 71 specimens from 18 sites.

Laos: Mekong drainage: XE BANGHIANG WATERSHED AND MEKONG MAIN RIVER: CMK 12853, 1; Khammouan Prov.: Mekong at Thakhek; 17°24'00"N 104°50'00"E. — CMK 13649, 5; Savannakhet Prov.: Houay Lapia, tributary of Xe Lanong entering it about 2 km downstream of Muang Nong; 16°22'29"N 106°29'11"E. — CMK 13720, 2; Savannakhet Prov.: Xe Bang Hiang at Keng Houapa, about 6 km downstream of Xepon; 16°40'14"N 106°11'40"E. — CMK 13794, 10; Savannakhet Prov.: Xe Bang Hiang at Ban Tat Hai Xe; 16°16'47"N 105°57'21"E. — CMK 13862, 3; Savannakhet Prov.: Mekong at Ban Pak Bo fisheries station, about 9 km north of Savannakhet; 16°38'36"N 104°45'15"E. Additional material: 40 specimens from 5 sites in Laos and 1 in Thailand.

Laos: Mekong drainage: XE DON WATERSHED: CMK 15877, 7; Salavan Prov.: Xe Set downriver of Ban Natou; 15°34'39"N 106°14'44"E.

Laos: Mekong drainage: XE KONG WATERSHED: CMK 15623, 10; Attapeu Prov.: creek entering Xe Kaman from north at Xe Kaman dam site; 14°57'40"N 107°09'16"E. — CMK 15671, 3; Attapeu Prov.: Nam Pa about 1 km upstream of Ban Paam; 14°55'56"N 107°03'00"E. — CMK 15807, 11; Sekong Prov.: Houay Cha Ngao, tributary of Xe Kong, entering it about 8 km upstream of Muang Kaleum; 15°46'08"N 106°45'54"E. — CMK 21536, 30; Sekong Prov.: Xe Nam Noy immediately below Taad Fek waterfall; 15°14'42"N 106°45'07"E. — CMK 21580, 3; Sekong Prov.: Xe Kong at Keng Chang rapids, near Ban Song Khone; 15°30'17"N 106°46'02"E. — CMK 21622, 5; Sekong Prov.: confluence of Houai Vi and Houai Nouan, 14 km upstream of Ban Kasang-Kang; 15°17'27"N 106°56'46"E. — CMK 21636, 15; Sekong Prov.: Houai Vi at Ban Kasang-Kang; 15°17'56"N 106°54'11"E. — CMK 23476, 1; Attapeu Prov.: Houay Soy (tributary of Xe Pian) at ford on road from Ban Mai to Pakxong; 14°47'54"N 106°25'00"E. — CMK 23525, 2; Attapeu Prov.: Xe Namnoy downstream of confluence with Houay Makchan; 15°08'00"N 106°40'16"E. Additional material: 81 specimens from 23 sites.

Diagnosis. *Mastacembelus dictyon* is distinguished from *M. armatus* [here, *M. armatus* refers only to populations from Northeast India], *M. pantherinus*, and *M. tinwini* by having fewer caudal-fin rays (13–15 vs 17–20 in *M. pantherinus*, 18–20 in *M. armatus* and *M. tinwini*) and fewer abdominal vertebrae (35–39 vs 41–44 in *M. armatus*, 42–44 in *M. pantherinus*, and 41–43 in *M. tinwini*). It is further distinguished from *M. armatus* and *M. pantherinus* by having fewer caudal (47–51 vs 51–55 in *M. armatus* and 54–57 in *M. pantherinus*), and total vertebrae (85–90 vs 93–98 in *M. armatus* and 97–100 in *M. pantherinus*), and by fewer dorsal-fin spines (33–37 vs 37–39 in *M. armatus*

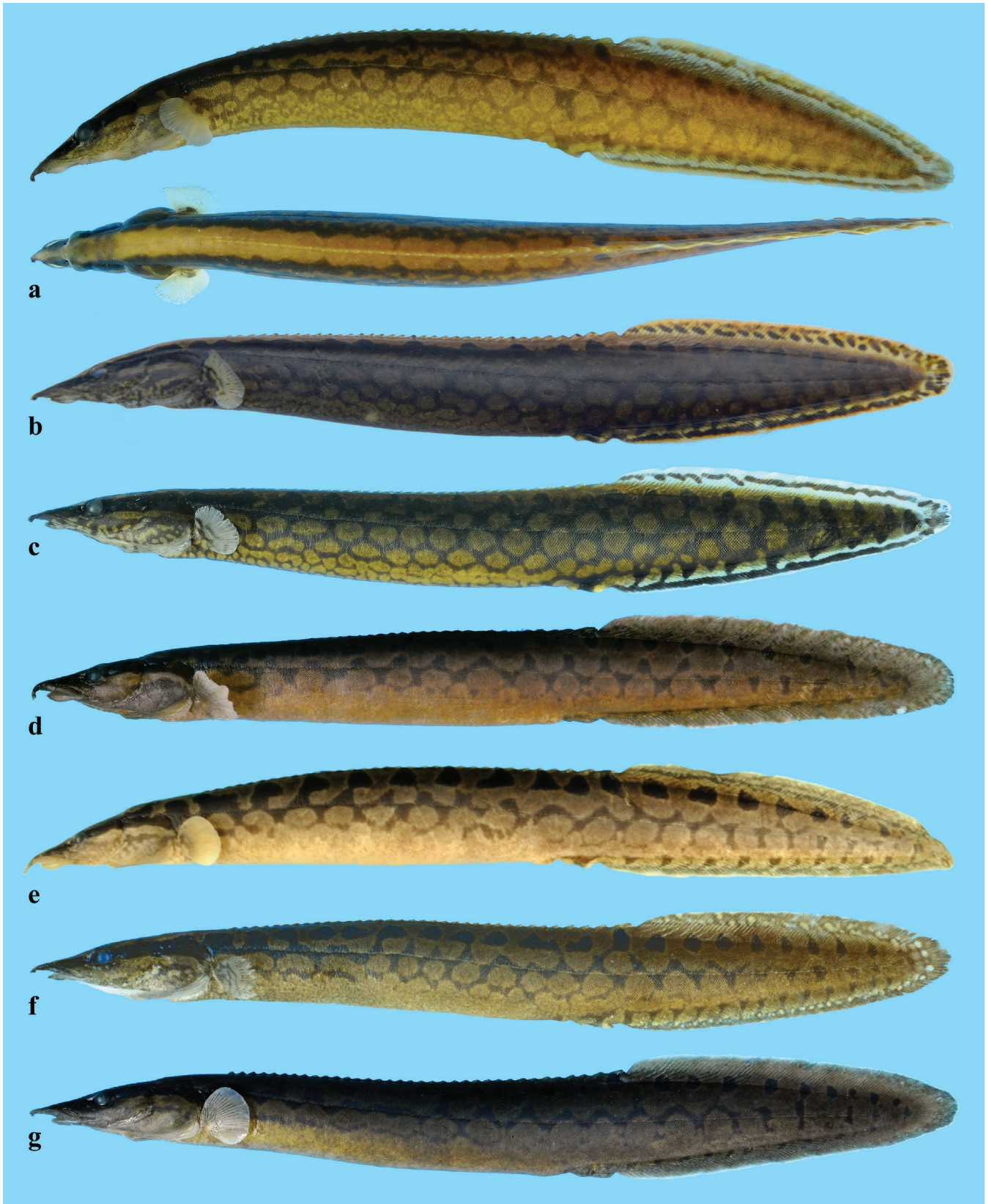


Fig. 7. *Mastacembelus dictyon*, Laos: Mekong drainage: Nam Ngiep (a–d) and Nam Ngum (e–g) watersheds. NAM NGIEP: a–b, CMK 27665, 101 mm SL (a, in lateral and dorsal view) and 119 mm SL (b, immediately after fixation); c, CMK 27544, 105 mm SL (reversed); d, CMK 24333, 269 mm SL. NAM NGUM: e, CMK 22427, 295 mm SL; f, CMK 13400, 116 mm SL (reversed); g, CMK 23823, 179 mm SL.

Table 1. *Mastacembelus dictyon*, selected morphometric data, based on holotype MHNG 2804.002, CMK22881 (n=2), 23823 (n=3), 24621 (n=1), 27524 (n=1), 27544 (n=1).

	N=10 (holotype)	mean± standard deviation
Standard length (SL) in mm	103–228 (170)	
In percent of standard length		
Head length (HL)	17.9–19.9 (18.4)	18.8±0.6
Predorsal length of spinous dorsal fin	20.1–21.9 (20.1)	21.1±0.6
Predorsal length of soft dorsal fin	63.9–69.1 (65.9)	66.2±1.5
Preanal length	58.4–64.4 (60.7)	61±2
Pectoral-fin length	5.0–6.2 (5.7)	5.6±0.4
Body depth at pectoral-fin base	6.8–8.3 (8.3)	7.6±0.4
Body depth at 1 st anal-fin spine	9.5–10.9 (10.9)	10.1±0.4
Body width at 1 st anal-fin spine	4.8–5.9 (5.9)	5.1±0.3
In percent of head length		
Snout length	31–35 (32)	32.6±1.4
Eye diameter	9–11 (11)	10.2±0.9
Ratios		
Depth/width of body	1.8–2.1 (1.8)	2.0±0.1
SL/HL	5.0–5.6 (5.4)	5.3±0.2
SL/body depth at 1 st anal-fin spine	9.2–10.5 (9.2)	10.0±0.4

and 37–40 in *M. pantherinus*). *Mastacembelus dictyon* can be distinguished from *M. thacbaensis* in having the first dorsal-fin spine pterygiophore inserted between the fourth and fifth neural spines (Fig. 4), rarely above the fifth neural spine (vs between fifth and sixth neural spines, rarely between fourth and fifth).

Specimens of *Mastacembelus dictyon* with more complete network of dark marking are also easily distinguished from *M. armatus*, *M. pantherinus* (Fig. 5), and *M. tinwini* (Fig. 6) by a different colour pattern, in which the body shows interconnecting bar series I–III and a network of dark markings surrounding light blotches on the belly (vs only interconnecting bar series II–III present and often restricted to posterior part of body and dark markings on belly absent or when present, only developed as longitudinal lines). *Mastacembelus dictyon* is further distinguished from *M. armatus* by having stripes c and d undulating, continued on head by irregular lines or markings or missing, interconnected by bars II, belly and head below stripe d paler brown than above, but not sharply contrasted with darker brown flank (vs straight and without bars II in their anterior part, continued straight on head, stripe c until tip of snout, and with belly and head below stripe d pale yellowish to whitish (in life), sharply contrasted with greenish brown area between stripes c and d; Fig. 14).

Mastacembelus dictyon has previously been confused with *M. fавus* because their dark and light colour markings appear similar on first inspection. However, the two species can be distinguished by details of the colour pattern, as follows (Fig. 3): specimens of *M. dictyon* with the most complete network of dark markings, which greatly resembles that of *M. fавus*, possess a continuous or almost continuous stripe b and series 1 of the lateral light blotches (vs stripe

b expressed as separate blotches only in contact with interconnecting bar series I; compare Fig. 3a with 3b); in specimens of *M. dictyon* with a less complete network, in which bar b is expressed as separated blotches, as in *M. fавus*, the ventrolateral and ventral parts of the body lack dark markings enclosing light blotches (vs network of dark markings present, enclosing light blotches); the blotches made by interconnection of stripes and bars are pale to dark brown, mostly not extending onto belly (vs blotches are pale brown to greyish, greatly contrasted against the dark brown to blackish stripes and bars, and usually extending onto belly); specimens of *M. dictyon* with the most reduced network (e.g., Fig. 11) can be readily distinguished from *M. fавus* in lacking some or all of the interconnecting bars of series I–III as well as the network of dark markings on the belly, which surrounds light blotches; dorsal, caudal and anal fins finely mottled or plain hyaline, with a thin blackish subdistal line, pale blotches not extending on fins, anal fin usually with vertically elongated marks continuing bars of series III (vs pale blotches conspicuously extending on dorsal and anal fins, wide subdistal line, connected with bars I and III [in specimens larger than about 100 mm SL]).

Description. For general appearance see Figs. 2, 7–12. Morphometric data are provided in Table 1 and meristic information in Tables 2 and 3. A species of the *Mastacembelus armatus* group, with elongate body, oval in cross section but strongly laterally compressed in caudal area. Depth 9.2–10.5 times in SL [holotype (HT): 9.2] and body width 1.8–2.1 times in its depth [HT: 1.8]. Up to at least 700 mm SL (field observation).

Head pointed, with median fleshy proboscis projecting from upper jaw; anterior naris at end of nasal tube originating at subdistal tip of nasal tentacle, rim of naris with two broad



Fig. 8. *Mastacembelus dictyon*, Laos: Mekong drainage: Nam Kading watershed: Nam Theun. a, CMK 12509, 124 mm SL; b, CMK 12786, 146 mm SL.

fimbriules and two narrow finger-like fimbriae; lips fleshy; jaws with numerous pointed but small teeth; gill membrane connected to isthmus; opercular opening large ventrally but extending dorsally only to level of horizontal through upper third of pectoral-fin base. Angle of preopercular region with three pointed spines of which upper largest; spines covered by skin.

Pectoral-fin rays 24–26 [holotype (HT): 25]. Dorsal fin with 35–39 [HT: 35] spines and 69–81 [HT: 81] rays. Anal fin with 3 spines and 67–82 (HT: 82) rays. Caudal-fin rays 13 (6+7 or 7+6) – 15 (7+8 or 8+7) [HT: 7+7=14]. Dorsal, caudal, and anal fins confluent. First dorsal-fin pterygiophore usually inserted behind 4th (rarely above 5th) neural spine, pterygiophore of last dorsal-fin spine inserted behind 39th, 40th, 41st, or 42nd [HT: 41st] neural spine. First anal soft-fin pterygiophore inserted behind hemal spine of 41st or 42nd [HT: 41st] vertebra.

Anal-fin spines covered by relatively thick skin, second spine longest, third completely concealed by skin. Penultimate dorsal-fin spine longest, followed by shorter last spine, concealed by thick skin, difficult to detect.

Lateral line extending from shoulder girdle in a horizontal line, following curvature of body, up to end of caudal peduncle. Vertebrae: 35–39 + 47–51 = 85–90 [HT: 38+48=86].

Colour in alcohol. Background colour pale to dark brown, sometimes darker brown, lighter toward vent. Head and body with black markings arranged in regular parallel series, expressed as (1) most complete pattern: a series of usually four (b–e), but up to five (b–f), stripes, mostly uninterrupted, undulating, interconnected via short vertical bars (series I–IV) forming a honeycomb or net pattern, with either some of the stripes or some of the interconnecting bars or both lacking in the caudal area of the body (e.g., Figs. 7c, 8). (2) reduced pattern: here longitudinal stripes often entirely missing (stripes e, f), reduced to series of blotches (stripes b, c), interconnecting bars missing (between stripes b and c, c and d). In its most reduced form (Fig. 11c) only remnants of stripes b, c, and d present, forming incomplete

series of roundish spots, of which only those of stripe b reach caudal area.

There are all kinds of gradual reductive changes between the complete and the most reduced pattern. In its most complete form (Figs. 7c, 8, 12a) the longitudinal stripes and vertical bars enclose longitudinal series of large light blotches, with blotch series 1 (between stripes b and c) comprising about 10–11 blotches in front of the dorsal fin, series 2 (between stripes c and d) up to 13 predorsal blotches. Blotch series 3 (between stripes d and e) is only present when stripe e is formed and may have up to 11 preanal blotches. When interconnecting bars and/or stripes are missing most of the body has only a light colouration (e.g. Figs. 10c, 11b, 12c).

In dorsal view, the incomplete stripe a is expressed as a series of elongate blotches between snout and nape. The back of the body has a lighter area along the series of dorsal-fin spines with the dark markings of stripe b sometimes extending to the dorsal midline (e.g. Figs. 7a, 9f).

In addition to these markings on the body, the head region has stripe c originating at the tip of the upper jaw from where it proceeds posteriorly through the eye and above the opercular region where the anterior end of stripe b merges with it. There are also several blotches and marbled lines on the opercular region and cheek below the level of the eye. This region is separated from stripe c on the head by a light area.

The pectoral fin is either uniform cream or has dark markings restricted to the base or continuing to the distal end of the fin in a more or less concentric arrangement. The soft portion of the dorsal fin has a light brown base with a series of dark blotches, representing a continuation of stripe b posteriorly. A median or subdistal dorsal-fin stripe may be developed, above which there is a hyaline to white distal margin. The anal fin has a light brown base with a series of small blackish blotches or spots, in the position of stripe e; these spots (bars) may be extended onto the fin as anteriorly oblique dark lines (e.g., Figs. 7c,e,f, 8, 9c,d, 12), equivalent to the series of bars III, which may sometimes fuse into a subdistal



Fig. 9. *Mastacembelus dictyon*, CMK 18139; Laos: Mekong drainage: Nam Kading watershed: Nam Theun. All specimens collected together. a, 55.1 mm SL (reversed); b, 57.7 mm SL (reversed); c, 104 mm SL (reversed); d, 126 mm SL; e, 165 mm SL; f, 186 mm SL.

stripe that sits on a cream coloured fin, which has a hyaline to white distal margin.

In juveniles under 100 mm SL, series 1–3 of light blotches often appear as a series of dark blotches with a lighter halo around them, a colouration that renders them less well separated from the dark network of stripes b–e and

interconnecting bars I–III (Fig. 9a, b). At around about 100 mm SL, the middle portion of the dorsal, anal and caudal fins is light cream and well distinguishable from their dark brown base and distal edge. A row of black blotches is often present on the base of the anal and soft dorsal fins. At this size, there may also be a black distal margin on these fins (e.g., Figs. 9c, 10a,b).



Fig. 10. *Mastacembelus dictyon*, Laos: Mekong drainage: Xe Bangfai watershed. a–b, lower Xe Bangfai, (a) CMK 23100, 78.1 mm SL (reversed); (b) CMK 19064, 143 mm SL (reversed); c–d, middle Xe Bangfai, exit of tunnel upstream of Ban Pakphanang, (c) CMK 12618, 115 mm SL; (d) CMK 17176, 162 mm SL; e, upper Xe Bangfai, CMK 12277, 177 mm SL.

See Discussion for further information on geographic and possibly habitat-related variability of the colour pattern.

Distribution. While we have examined material from the Mekong drainage only in Thailand, Laos, and Cambodia, the species is expected also in Vietnam. Records of *M. armatus* from the Mekong drainage in China by Yang & Zhou (2011) probably refer to *M. dictyon*.

Etymology. The name is derived from the Greek word δίκτυον (*dictyon*), net, referring to the network of dark interconnected lines on the body. A noun in apposition.

Remarks. *Mastacembelus dictyon* has previously been referred to as *M. armatus* (e.g., Rainboth, 1996; Rainboth et al., 2012: fig. 1127; Kottelat, 1998, 2001a, 2011, 2016; Vidthayanon, 2008; Phousavanh, 2017) or as *M. favus* (e.g., Rainboth et al., 2012: fig. 1131; Jamaluddin et al., 2019, 2021; Duong et al., 2020).

DISCUSSION

The *Mastacembelus armatus* group is often considered difficult taxonomically: Kottelat (2013) listed no fewer than 10 available names in the synonymy of *M. armatus*. The difficulties seem to stem from two main sources: *M. armatus* and its close relatives undergo significant developmental changes in colour pattern from juveniles to adults (see Britz, 2007: fig. 5; this paper, e.g., Fig. 9), and there is substantial variation in the colour pattern even among adult individuals at the same locality (see Britz, 2007: fig. 2 and fig. 3c; this paper Fig. 9). Developing a standardised terminology for the markings in the *M. armatus* group, combined with counts of vertebrae and dorsal-fin spines and rays, was crucial in Britz's (2007) revision of Myanmar species. The same approach applied here enabled us to diagnose *M. dictyon* from other species of the *M. armatus* group.

Hereunder, *M. armatus* refers only to the species known from India and Myanmar to which belongs the neotype designated below. This identity excludes all the records from Thailand, Cambodia, Laos, Vietnam, and China that have



Fig. 11. *Mastacembelus dictyon*; Laos: Mekong drainage: Xe Banghiang watershed and Savannakhet. a, CMK 13649, 162 mm SL; middle Xe Banghiang (reversed); b, CMK 13794, 139 mm SL; lower Xe Banghiang; c, CMK 13862, 110 mm SL; Mekong near Savannakhet.

previously been referred to by this name. The easiest way to distinguish *M. dictyon* from Indian and Myanmar specimens of *M. armatus* is by the number of vertebrae. *Mastacembelus dictyon* has fewer abdominal (35–39 vs 41–44), caudal (47–51 vs 51–55), and consequently total vertebrae (85–90 vs 93–98). There is also a clear difference in the number of caudal-fin rays, with *M. dictyon* having a smaller caudal fin with only 13–15 rays compared to a wider caudal fin with 17–20 rays in *M. armatus*. *Mastacembelus dictyon* also has fewer dorsal-fin spines (33–37) than *M. armatus* (37–39). A lower number of abdominal vertebrae distinguishes *M. dictyon* also from *M. pantherinus* and *M. tinwini* (35–39 vs 42–44 and 41–43, respectively). The colour pattern of *M. dictyon* with its network of dark markings and enclosed light blotches easily distinguishes it from *M. armatus*, *M. pantherinus*, and *M. tinwini*. In *M. armatus* (Fig. 14), stripe b is expressed only as a series of round blotches, and in addition bars of series I are often missing at least in part of the abdominal region; *Mastacembelus pantherinus* (Fig. 5) does not have any stripes but instead numerous individual dark spots or irregular marks, while in *M. tinwini* (Fig. 6) the stripes a–e are expressed either as complete or interrupted stripes or as series of blotches or as a combination of both without any of the interconnecting bars of series I–III (Britz, 2007). There are, however, some specimens of *M. dictyon* with the reduced network pattern that may resemble *M. armatus* (Figs. 10c, 11a). These *M. dictyon* can easily be distinguished from *M. armatus* by the meristic differences mentioned above.

As mentioned in the description, there is much variation in the colour pattern of adult *M. dictyon*. There is no clear relationship between colour pattern and geographic distribution or size (age); there is possibly some relation with

habitat. Various degrees of colour-pattern ‘completeness’ may be observed at a given site. For example, we have observed hundreds of specimens from undisturbed habitats in the Nam Theun watershed, a branch of the Nam Kading, a tributary of the Mekong, in which most of the specimens have a complete reticulated pattern (Fig. 9 illustrates specimens collected together). Only a few exhibit a pattern that is incomplete (Figs. 9d, e), or relatively indistinct against a very dark background. There is, however, an apparent association between the most incomplete pattern, a pale background colour, and more lowland and large river habitats such as in the Xe Banghiang watershed (Fig. 11). There, stripe b is relatively indistinct and stripes d–f may be missing, as well as the bars of series II–V and blotches of series 2–4. But specimens with such incomplete pattern were not restricted to these habitats and drainage, and not all specimens in this drainage and habitats had this incomplete pattern. This may reflect a collecting bias in the different drainages (material from the Nam Ngum, Nam Ngiep, Nam Kading, and Xe Bangfai watersheds had mainly more or less complete pattern, were mainly obtained during work in middle and upper sections of the rivers; in rapids, on stone to rocky substrate, generally in shaded areas), while the Xe Banghiang material, which had mainly incomplete patterns, was obtained during work in the lower section, on sandy habitats. This incomplete pattern was also observed in a few specimens from the Mekong main river. In the Xe Bangfai, specimens in the upper part of the watershed have the complete pattern (Fig. 10a, b) while specimens from the lower Xe Bangfai (Mekong floodplain) have an incomplete pattern, in which stripes c and d are complete and stripe e is missing: stripe b may be missing, or interrupted, sometimes appearing as dark blotches continuing some bars of series I until the base of dorsal-fin spines; and the blotches along



Fig. 12. *Mastacembelus dictyon*, Laos: Mekong drainage: Xe Kong watershed. a, CMK 15623, 86.8 mm SL; b, CMK 15671, 150 mm SL; c, CMK 15807, 161 mm SL; d, CMK 23476, 167 mm SL (reversed).

the base of the soft dorsal fin are distinct (Figs. 10c–e). Somewhat similarly patterned specimens are also present in the Nam Ngum and Xe Kong (Figs. 7g, 12c).

Mastacembelus favus (Figs. 3b, 13) comes close to *M. dictyon* in terms of meristic characters (Tables 2, 3) and colour pattern. It was described by Hora (1923) from Thailand and later reported from Malaysia, Laos, Cambodia, and Vietnam. The name has also been used for fishes from the Mekong drainage. Distinguishing *M. dictyon* from *M. favus* is not always easy, because they show similar ranges in the number of vertebrae and dorsal-fin spines and rays and *M. dictyon* has a great variation in colour pattern. This ranges from an extensive network of dark markings resembling that of *M. favus*, through various degrees of reduction of individual elements of dark markings to an almost complete absence of these markings. Distinguishing *M. favus* from individuals of *M. dictyon* with these reduced patterns is straightforward. The more complete network pattern of *M. dictyon* differs from that of *M. favus* in that it is more regular, the stripes are clearly aligned, the blotches are smaller and paler (background colour is brown, vs yellowish brown to grey, sometimes bright yellow in life, with stripes and interconnecting bars very contrasted). Besides, *M. dictyon* shows an additional series of light blotches, series I, separated by the interconnecting bars of series I, and dorsally bordered by a more or less continuous stripe b. In *M. favus*, stripe b is not continuous and consists only of a row of roundish dark brown to black marks that are confluent with the interconnecting bars of

series I; thus the light blotches of series I are absent or can be considered continuous with those between stripe b and the dorsal midline. Generally, *M. dictyon* appears slenderer than *M. favus* (not quantified; see Roberts, 1986: 106). In *M. dictyon*, the belly is plain yellowish or brown, with or without irregular mottling, or lines, sometimes continuing the reticulated pattern with irregular blotches continuing series 4 (Figs. 7b,c, 8). In *M. favus*, the reticulated pattern extends on the whole belly, with clearly distinct roundish blotches.

Three recent papers (Jamaluddin et al., 2019, 2021; Duong, 2020) looked at the molecular diversity of what they referred to as *M. favus*. They identified two clearly separated units, one (“lineage 1” in Jamaluddin et al., 2019 and “Group 1” in Jamaluddin et al., 2021) distributed from the Malay Peninsula north to the Chao Phraya and east to the lower Mekong and the other (“lineage 2” in Jamaluddin et al., 2019, “Group 2” in Jamaluddin et al., 2021) restricted to the middle and upper Mekong. Unfortunately the authors did not provide images or data of their specimens that would have allowed them to be linked with one or the other unit. But based on the distribution, however, it seems likely (but not certain) that their first lineage corresponds to *M. favus* and the second to *M. dictyon*.

Although *M. favus* is known from the lower Mekong (Rainboth et al., 2012: fig. 1130; So et al., 2019: 134, upper figure), some records are ambiguous (e.g., Rainboth, 1996: fig. p. 180 is from Sufi, 1956 [itself copied from Hora, 1924]

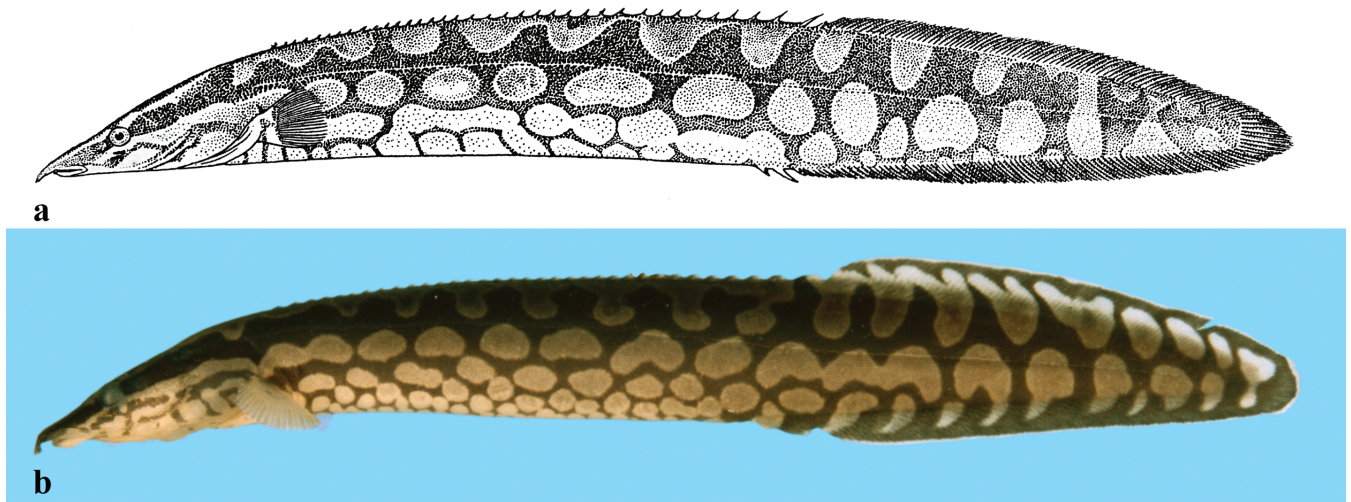


Fig. 13. *Mastacembelus favus*. a, lectotype (from Hora, 1924: fig. 2); b, CMK 20188, 126 mm SL; Thailand: Chantaburi: Mekong drainage, Tonle Sap basin.

and shows the lectotype; the actual basis for the record is not known; but pl. 24 fig. 185 shows *M. dictyon*). The actual extent of *M. favus* in the Mekong drainage downstream of Khone Falls is not clear; at least it is not present in our sampling from the Xe Kong watershed in Laos, where MK observed only *M. dictyon* (29 sites). Baird et al. (1999: 130, fig. 269 right) illustrate a specimen from an unspecified locality in southern Laos that is possibly *M. favus*.

In the Mekong drainage, upstream of Khone Falls, *M. favus* is recorded in Thailand by Roberts (1986) from Khon Kaen and the market at Ubon Ratchatani. He figured the last sample (Roberts, 1986: fig. 2d), stored now at the Swedish Museum of Natural History under NRM 45925. The origin of the specimen of *M. favus* figured in Grudpan et al. (2023: 94) is not explicitly stated. CMK 20188 (Figs. 3b, 13c), although from the Mekong drainage in Thailand, is from a stream draining to Tonle Sap in the lower Mekong in Cambodia. Specimens figured in Nagao Natural Environment Foundation (2020: 350, figs. B, I) are apparently *M. favus* from the lower Mekong in Vietnam; their Fig. A shows market specimens from Vientiane, apparently *M. dictyon*, as well as their other photographs identified as *M. armatus*. Other records of *M. favus* from the Mekong drainage in Thailand include several localities listed by Khachonpisitsak (2007: 118): Chiang Rai, Nong Khai, Songkhram River, Sakon Nakhon, Ubon Ratchatani, Nakhon Ratchasima; she included pictures of specimens of *M. favus* from Nan (Chao Phraya drainage) but no illustration of her material from the Mekong drainage.

***Mastacembelus favus* lectotype designation.** *Mastacembelus favus* was described by Hora (1923) based on material from lake Talé Sap (Phattalung province, peninsular Thailand) and Nontaburi (north of Bangkok). Hora (1924) illustrated one of these specimens without providing locality information for it. The illustrated specimen shows the characteristic colour pattern that we found in other specimens of *M. favus*: stripe b expressed not as a continuous stripe but as a series of dark roundish marks that are connected to stripe c by interconnecting bars of series I, large blotches in

series 2, and a network of dark markings on the belly (Fig. 13a). We therefore select the specimen illustrated by Hora (1924: fig. 2) as the lectotype of *M. favus*. At this stage, we have no way to find out the locality of this specimen, but given the difficulty of distinguishing some examples of *M. armatus* from *M. favus*, there is a risk that the type series (five specimens from 2 localities) includes more than a single species. We designate the figured specimen as lectotype to retain the name for this species and thereby stabilise its identity. At least one of the syntypes is in ZSI (Sufi, 1956: 138); it was listed as ZSI F 10340/1 in Menon & Yazdani's (1969) catalogue of types in ZSI. They list it as holotype, but it is a syntype. It is not known whether or not this is the specimen figured by Hora (1924). We have not yet been able to obtain information on the locality from which the lectotype had been collected. Presently the ZSI syntypes cannot be traced (L. Kosygin, pers. comm.). Our Fig. 13b shows a specimen from the Mekong drainage near Chantaburi (Thailand) very similar to that figured by Hora (1924: fig. 2).

***Mastacembelus armatus* neotype designation.** La Cépède (1800: 286) described *Macragnathus armatus* based on a single specimen, 360 mm total length. No locality was mentioned, the only information is that the specimen came from the cabinet of the Stadhouder [natural history collections of the Governor of Holland], 'ceded' by Holland to [= seized by] France when it invaded Holland in 1793. Part of the material was returned to Holland, but fishes remained in MNHN (Bauchot et al., 1996). Bauchot & Daget (1996) listed the species described by La Cépède based on material from the Stadhouder collection and mentioned whether the types, if any, were present in MNHN. *Macragnathus armatus* is not on the list.

It is often assumed that most material of the Stadhouder collection came from the East Indies, but this cannot be the rule for the fishes. For most species he described, La Cépède (1800) mentioned that the origin was not known, or he simply made no mention. Cuvier & Valenciennes (1828–1849) made

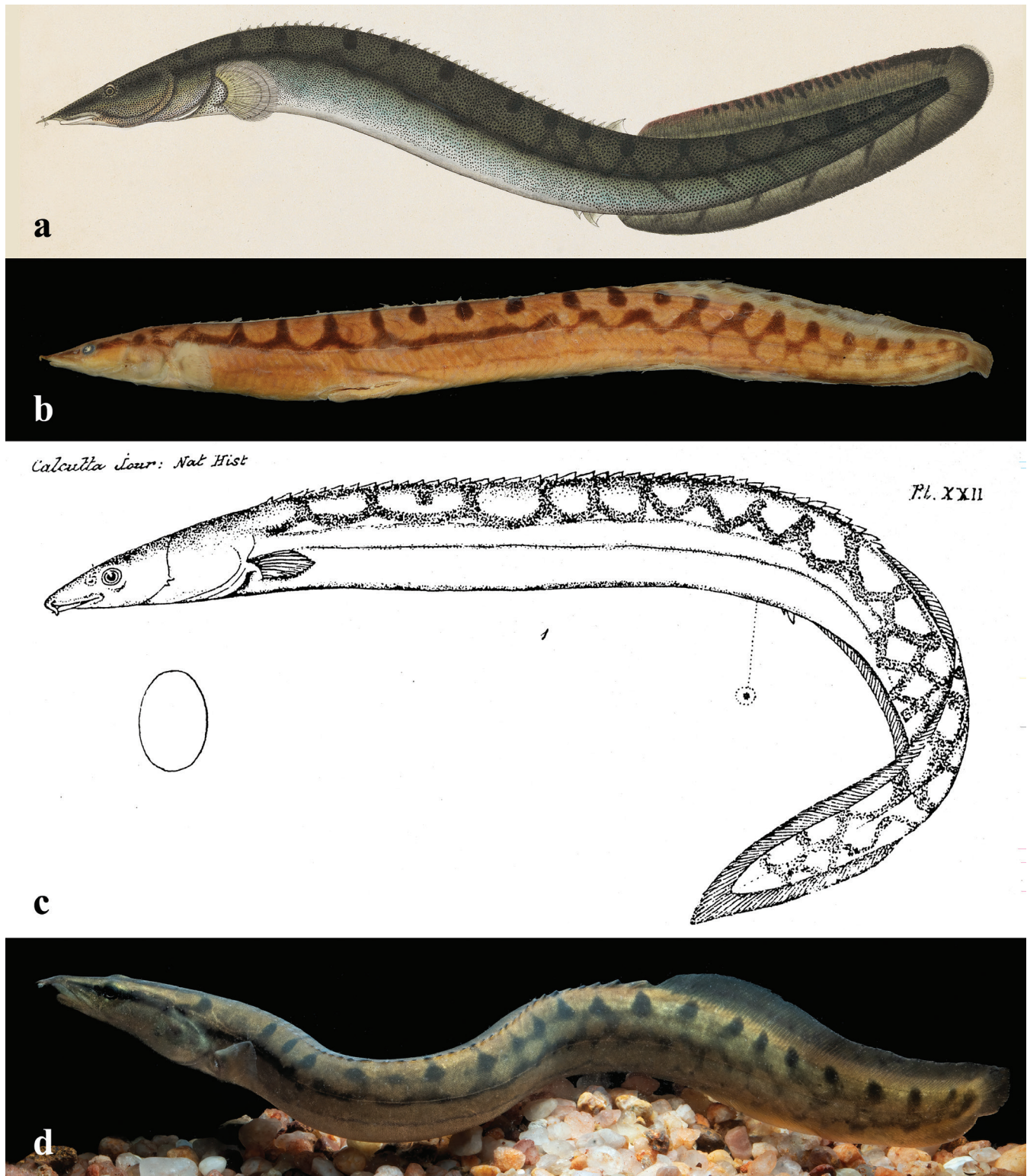


Fig. 14. *Mastacembelus armatus*; a, Haludat's coloured illustration, printed in b&w in Hamilton (1822), specimen from Lukhipur (now Lakshmipur, Bangladesh) or Baruipur (West Bengal, India), see Britz (2019, p. 26) (photograph: K. Webb, from the archive of the British Library [Mss Eur E72, p. 90]); b, NRM 69592, neotype, 170 mm SL; India: Ganga River basin, Tumapao (= Duma Baor) River close to Duma village (photograph: S.O. Kullander); c, figure of *M. undulatus* in M'Clelland (1844a: pl. 22 fig. 1); d, not preserved, ca. 250 mm SL; India: West Bengal: Sankosh River (photograph: B. Mahatvaraj).

reference to the material from the Stadhouder collection mentioned by La Cepède (1800), and examined some. Bauchot & Daget (1996) compiled the list of La Cepède's species based on material of the Stadhouder collection and listed which of this material was present in MNHN's

collections and what Cuvier & Valenciennes said about them. From the list compiled by Bauchot & Daget, the origin of two species is given as 'seems to be from Moluccas', two as 'Surinam', one as 'Grandes Indes' [an archaic wording for East Indies], one as 'probably originating from Java'.

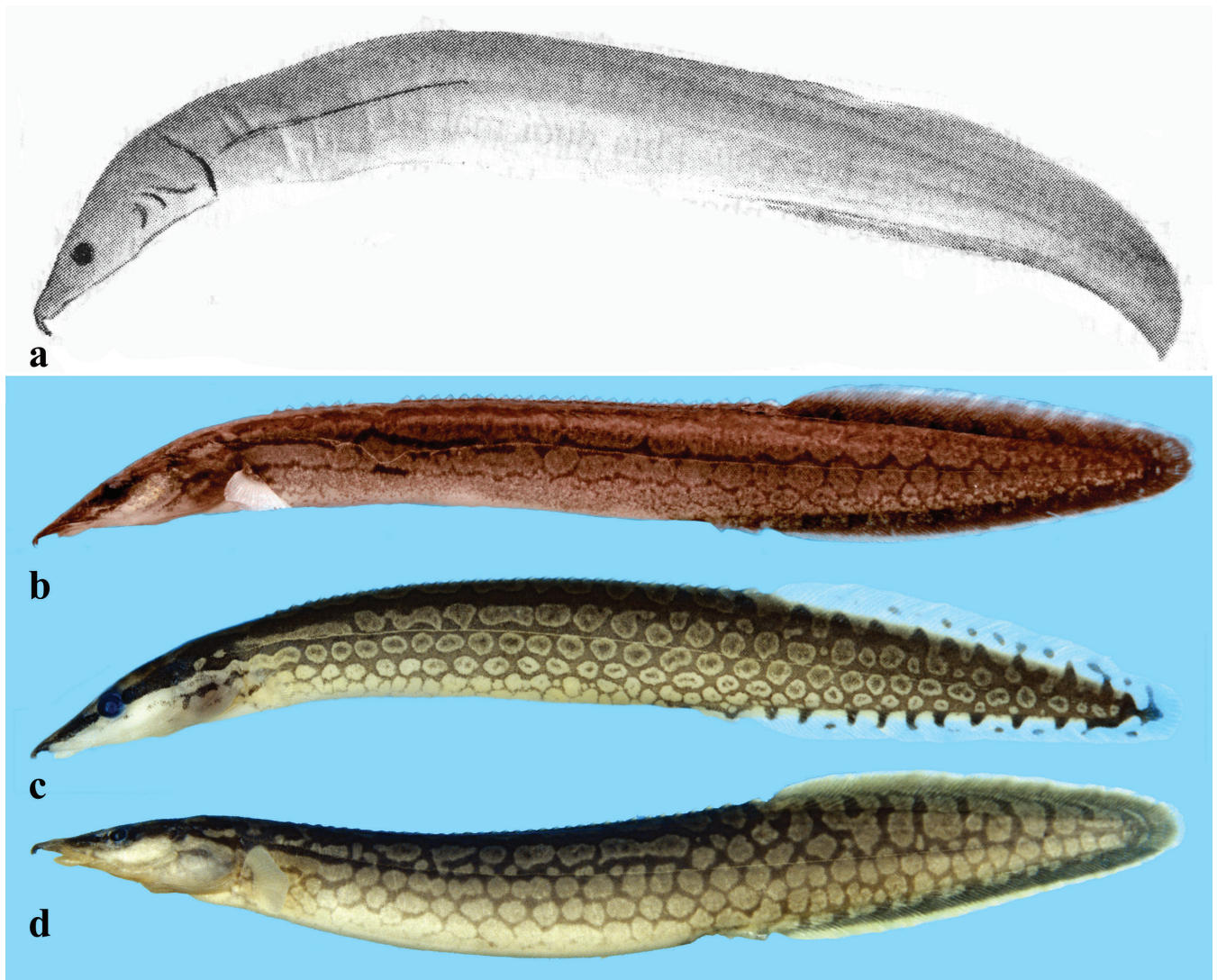


Fig. 15. *Mastacembelus thacbaensis*; northern Vietnam; a, possibly holotype, 392 mm SL; Yen Bai Province: Thac Ba (from original description, Nguyen, 2006: 633, fig. 4); b, MK 99-120, not preserved, 141 mm SL; Tuyen Quang Province; c, CMK 14882, 76 mm SL; Quang Ninh Province, Mong Cai; d, CMK 14882, 196 mm SL; Quang Ninh Province, Mong Cai.

La Cèpède (1803: 50) also described *Ompok siluroides* from the collection of the Stadhouder. He did not mention the origin. He mentions “an inscription attached to this individual indicated that the name given to this species in the country it inhabits was ompok”. ‘Ompok’ is apparently an erroneous transcription, or a misreading of limpok, which is still the name of a number of species of *Ompok* and *Kryptopterus* in Indonesia (Weber & de Beaufort, 1913: 210; Kottelat et al., 1993: 70; Kottelat, 2013: 236). At that time, freshwater fish material from Southeast Asia, received in the Netherlands, did not usually originate from elsewhere than Batavia [Jakarta], on Java. *Ompok siluroides* is distributed throughout Southeast Asia (Ng & Hadiaty, 2009: 56). Therefore the inference is that the type locality of *O. siluroides* is probably Batavia, a conclusion already reached by Bleeker (1858: 304) and that the Stadhouder’s collection indeed included at least one freshwater fish species from Java.

However, the situation is not always that straightforward. For *Cheilodactylus fasciatus*, La Cèpède gave a local name as “Ikan kakatora itam, dans les Indes Orientales”; Cuvier

(in Cuvier & Valenciennes, 1830: 359) disagreed and commented that he was “certain” that the specimen came from near Cape Town. The vernacular name indicated by La Cèpède is Malay (ikan = fish, itam = hitam = black) and supports a Southeast Asian origin [but nobody knows where La Cèpède obtained this name]. Cuvier also commented that the specimen examined and used by La Cèpède is the same as described and figured by Gronovius (1763: 64, no. 221, pl. 10 fig. 1) as *Cynaedus*, from “Oceano Indico. D. D. Arnoldi Vosmaeri”. “Oceano Indico” should not be understood exactly as the modern Indian Ocean; Arnout Vosmaer (1720–1799) was director of the Stadhouder collection from 1756 to 1795 (Rookmaaker, 1989: 120). Bauchot & Desoutter (1989: 10) and Bauchot & Daget (1996: 233) listed the holotype as MNHN A.169, a dried skin, right side (La Cèpède and Gronovius show a left side). On 11 November 2025, the online Catalogue of Fishes mentions this specimen as material of Castelnau, which does not make sense; it mentions also the holotype as RMNH 2759, with a reference to Russell & van Oijen (2021: 429). These authors list RMNH 2759, without mentioning a type status; this is a specimen collected



Fig. 16. *Mastacembelus thacbaensis*, Laos: Houaphan Province: Nam Ma drainage. a, CMK 15396, 34.3 mm SL; Nam Ma; b, CMK 25820, 122 mm SL; Nam Xam; c, CMK 25820, 196 mm SL; Nam Xam; d, CMK 25698, 330 mm SL; Nam Ma.

by Castelnau at the Cape of Good Hope (Cape Town, South Africa; then a Dutch colony) and mentioned by Bleeker (1859: 63). *Cheilodactylus* includes only two species, and the range of the genus is from Namibia to Natal (Burrige & Smolenski, 2004; Kimura et al., 2018; Ludt et al., 2019). The recent revisions of the family have not examined the type material or discussed identification issues (Burrige & Smolenski, 2004; Ludt et al., 2019).

This long digression serves to show that the Stadhouder collection included fish material from at least the East Indies, Mollucas, Java, Cape of Good Hope and Surinam, without formally excluding other Dutch colonies, dependencies and trading posts ('factories'), of which there were many around the coast of India and Sri Lanka (https://en.wikipedia.org/wiki/Dutch_Bengal).

A number of the specimens from the Stadhouder collection used by La Cépède are still in MNHN and were later reported by other authors, e.g., Cuvier & Valenciennes (see above). But when redescribing *M. armatus*, Cuvier (in Cuvier & Valenciennes, 1832: 456) did not mention the holotype and it was presumably already lost. Interestingly, on page 459, Cuvier mentioned a single specimen about the same size (MNHN A.5431, 360 mm SL <http://coldb.mnhn.fr/catalognumber/mnhn/ic/a-5431>), collected by Pierre Sonnerat in Pondicherry [Puducherry], India. Sufi (1956: 138) listed this specimen as holotype of *M. armatus*. An incorrect

identification and/or cataloguing of the holotype of *M. armatus* as this specimen seems excluded by the mention by La Cépède that he counted the rays on both pectoral fins. It cannot be the specimen attributed to Sonnerat, because this is a dry fish mounted on a wood plate with a single pectoral fin visible. Cuvier (in Cuvier & Valenciennes, 1828: 124) mentioned that when Sonnerat "returned to France in 1814, he gave us the fishes that he had assembled [in Pondichéry] dried as done by Commerson and Gronovius [= herbarium sheets; Cuvier & Valenciennes, 1828: 101, 123, Wheeler, 1958]". More on Sonnerat can be found in Rookmaaker (1989: 37).

After the original description by La Cépède, the species *M. armatus* was first recognised by Hamilton (1822: 28, pl. 37 fig. 6; reproduced by Britz, 2019: pl. 18 [not 10]; here Fig. 14a). He published the first illustration of the fish, based on a specimen he collected and had illustrated while he was stationed at Lukhipur (now Lakshmipur in Bangladesh) on the lower Meghna or Baruiapur, just south of Calcutta. Since, and especially after the redescription by Cuvier (1832), the name has been associated mainly with material from India (see extensive list of citations in Sufi, 1956: 134) and we consider it desirable to retain the name for the species from the lower Ganges/Meghna system. [En passant, this area also includes some Dutch colonial trading posts, e.g., Chinsurah on the Hooghly estuary; <https://en.wikipedia.org/wiki/Hugli-Chuchura>, https://en.wikipedia.org/wiki/Dutch_Bengal].



Fig. 17. *Mastacembelus thacbaensis*, Laos: Xiangkhouang Province: Nam Neun drainage. a, CMK 25873, 98 mm SL; Nam Neun; b, CMK 15284, 124 mm SL; Nam Mat; c, CMK 29028, 193 mm SL; Nam Mat; d, CMK 28998, 175 mm SL; Nam Mat (immediately after fixation).

With only speculations on the possible type locality and history of the holotype of *M. armatus*, the early disappearance of the holotype, the imprecise and uninformative original description, the absence of an illustration, and many species sharing the few characters mentioned by La Cépède, we are unable to objectively establish to which species the holotype of *M. armatus* belongs. It is necessary to designate a neotype to definitively link the name to one of these species.

We designate NRM 69592 as neotype of *M. armatus* (Fig. 14b). It was collected in the Ganga River drainage at Calcutta on 14 February 1934 by R. Malaise. It has 38 dorsal-fin spines with the insertions of its associated pterygiophores between neural spines 4/5 and 45/46, it has 78 dorsal-fin rays, 80 anal-fin rays, 9+10 caudal-fin rays, 24 pectoral-fin rays, and 42 abdominal and 55 caudal = 97 total vertebrae. It satisfies all the conditions for neotype designation required by the *Code* (article 75.3.1–7): it is designated to clarify the taxonomic status and the type locality of the nominal taxon *M. armatus*; the loss of the original holotype and the unknown original locality are discussed above; and the neotype is stored in the Naturhistoriska Riksmuseet, Stockholm, Sweden.

The neotype agrees with Hamilton's illustration (1822: pl. 37, Fig. 6, reprinted in colour in Britz (2019: pl. 18) and reproduced here as Fig. 14a) in major features of the colour pattern (stripe b reduced to a series of blotches, stripe c

well expressed and connected to blotches of stripe b by bars of series I in caudal region, bars of series II present but restricted to caudal region) and the number of dorsal-fin spines and rays (Hamilton: about 37 dorsal-fin spines and 83–85 rays and 88–90 anal-fin rays, 17 caudal fin rays, pectoral-fin rays 21 branched; neotype, NRM 69592: 38 dorsal-fin spines, 78 dorsal-fin rays, 80 anal-fin rays, 19 caudal-fin rays including unbranched rays, pectoral-fin rays 24 including unbranched rays).

M'Clelland (1844a: 393, 398) commented that Hamilton's *M. armatus* cannot be the same as La Cépède's because it had more dorsal-fin spines (33 in La Cépède vs 37 in Hamilton's text, 36 on figure) and he proposed a new name for Hamilton's species (*M. hamiltonii*). La Cépède mentioned that the specimen was not in a good state; and we do not know how reliable La Cépède's description is (others of his descriptions have created problems), it is not possible to evaluate the reliability of this information. In addition, our material of *M. armatus* has the number of dorsal-fin spines range from 36–38 with the first one or two spines difficult to detect if depressed and with the last dorsal-fin spine often concealed by the penultimate spine and frequently overlooked.

Since the name *M. armatus* is now linked to the only species of *Mastacembelus* known from the Ganges drainage, *M. hamiltonii*, whose type material is from an unspecified locality

Table 2. Vertebral numbers of different species of the *Mastacembelus armatus* complex. *Mastacembelus dictyon* based on MHNG 2804.002 (holotype, values marked with asterisk), CMK 22881, 24621, 27544, 27664, 28082, 21536, 21580, 23476, 23525, 19272, 23823, 26057, 19252, 26018, 25967 (n=55); *M. pantherinus* (n=18) and *M. tinwini* (n=31) from Britz (2007); *M. armatus* based on NRM 24789, 40430, 69592 (n=5); *M. thacbaensis* based on ANSP 210057, 212196, NRM 49681, 49682, 49683, 49684 (n=7); *M. favius* based on CMK 4871, NRM 24795, 45925 (n=4).

	abdominal										caudal										total																
	36	37	38	39	40	41	42	43	44	47	48*	49	50	51	52	53	54	55	56	57	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>M. dictyon</i>	2	10	35*	8						3	10*	18	12	3							6	11*	17	9	3	1											
<i>M. pantherinus</i>						2	11	5								1	4	2	2														2	2	3	2	
<i>M. tinwini</i>				6	13	11	1	2	2	2	9	9	6	1										2	4	5	8	5	4	1							
<i>M. armatus</i>					2	3								1	2	2	1													1	1	1	1				
<i>M. favius</i>			1	3							1	2	1									1		2	1												
<i>M. thacbaensis</i>				5	2						1	1	3											1	4												

in the Ganges drainage, becomes a subjective synonym. The available information does not allow to dispute this identification, and thus no neotype for *M. hamiltonii* is necessary.

Identity of *Mastacembelus undulatus*. The name *M. undulatus* has been linked with populations of the *M. armatus* group from Southeastern China and Vietnam. M'Clelland (1844a) reported on a collection of fishes by G. R. Playfair made in China at Chusan Island (correctly Zhoushan Dao) and Ningpo (correctly Ningbo), in Zhejiang, opposite Zhoushan island. Playfair was part of a military expedition (known in the West as the First Opium War) from 1839 to 1843, and he is unlikely to have had the opportunity to travel outside this area.

Among this material, M'Clelland described *Macrognathus undulatus*, reportedly from Zhoushan. The Chinese origin of part of this collection was doubted by Rendahl (1927: 180) and Ng & Kottelat (2005: 18). Rendahl (1927) considered that *M. undulatus* was based on material of Indian origin.

Ng & Kottelat (2005) examined the list of species reported by M'Clelland (1844a) and concluded that some of the species he reported from China are indeed known from China (assuming that they were correctly identified), but others are obviously either misidentified or mislabelled and belong to well-known Indian genera, unknown in northern and eastern China. From this list, it appears that most of the freshwater species reported from Chusan are in fact known from India or Myanmar and unknown from China. We therefore conclude that the material must have been mixed or mislabelled and that the type locality of *M. undulatus* is probably in India. In support of this hypothesis, we note that M'Clelland (1844a) listed 20 caudal fin rays for his *M. undulatus*, a count that is common in Indian *Mastacembelus*, but not in the Chinese species, which has only 14–16 (see Table 2). To our knowledge, the northernmost record of a *Mastacembelus* in China seems to be in Fujian (Chu, 1985: 447).

The whereabouts of the material described by M'Clelland (1844a) is not known (Sufi, 1956: 138). Some of the material described in his other works (M'Clelland, 1838, 1839, 1842, 1844b) are in BMNH, SMF, and ZSI (e.g., Günther, 1859: v), but disposition of the material described in the 1844a paper is unknown and it is presumed lost. The species is also not mentioned by Menon & Yazdani (1969: 161). The first author searched the collections of BMNH without locating the type and although SMF has material of *M. armatus* from M'Clelland, this was collected in 1847.

No type of *M. undulatus* is known to survive; nor has ever been mentioned. Different species of the *M. armatus* group exist in China and India that agree with the limited original description and figure (here reproduced as Fig. 14c) and there is no objective criterion to establish the identity and origin of M'Clelland's material of *M. undulatus*. Endruweit (2024: 109, fig. 216a) designated as neotype for *M. undulatus* ANSP 210057-5080 (locality: Ninh Binh, Hoa Lu, Red River delta). The *Code* art. 75.3 requires that a neotype designation

Table 3. Dorsal-fin spine numbers of different species of the *Mastacembelus armatus* complex. *Mastacembelus dictyon* based on MHNG 2804.002 (holotype, values marked with asterisk), CMK 22881, 24621, 27544, 27664, 28082, 21536, 21580, 23476, 23525, 19272, 23823, 26057, 19252, 26018, 25967 (n=49); *M. pantherinus* (n=18) and *M. tinwini* (n=31) from Britz (2007); *M. armatus* based on NRM 24789, 40430, 69592 (n=5); *M. thacbaensis* based on ANSP 210057, 212196, NRM 49681, 49682, 49683, 49684 (n=7); *M. favus* based on CMK 4871, NRM 24795, 45925 (n=4).

	dorsal-fin spines						
	34	35	36	37	38	39	40
<i>M. dictyon</i>	1	15*	28	5			
<i>M. pantherinus</i>				1	6	7	4
<i>M. tinwini</i>				4	16	9	2
<i>M. armatus</i>				2	3		
<i>M. favus</i>		1	3				
<i>M. thacbaensis</i>		2	5				

must include “evidence that the neotype is consistent with what is known of the former name-bearing type from the original description and from other sources” (art. 75.3.5). The figure of the holotype in M’Clelland (1844a: pl. 22 fig. 1), however, shows a fish with a colour pattern conspicuously different from that of Endruweit’s (2024) intended ‘neotype’. The *Code* also requires “evidence that the neotype came as nearly as practicable from the original type locality” (art. 75.3.6); we know that the holotype came from Chusan or India and designating a specimen from Vietnam as neotype violates art. 75.3.6. While there is no material available from Chusan (because the species does not exist there) there are plenty of specimens from northern India of ‘practicable’ access in several museums, which are suitable for a neotype designation. Endruweit’s (2024) neotype designation for *M. undulatus* is thus invalid.

The identity of *M. undulatus* cannot be resolved given that the type locality remains unknown. Further, several species previously identified as *M. undulatus* are now without valid name. It is thus necessary to designate a neotype. We designate NRM 69592 as neotype. This is the specimen designated above as neotype of *M. armatus* and this makes the two names objective synonyms. It satisfies all the conditions for neotype designation required by the *Code* (article 75.3.1–7); it is designated to clarify the taxonomic status and the type locality of the nominal taxon *M. undulatus*; the loss of the original holotype and the unknown original locality are discussed above; and the neotype is stored in the Naturhistoriska Riksmuseet, Stockholm, Sweden. The neotype of *M. undulatus*, NRM 69592, matches M’Clelland’s (1844a) description of *Macrognathus undulatus* closely in the reported counts and colour pattern (Fig. 14c,d).

***Mastacembelus ‘undulatus’* in Laos and Vietnam.** With stabilisation of the name through a valid neotype designation, the identity of a species of *Mastacembelus* from northeastern Laos and Vietnam identified as *M. undulatus* (e.g., Kottelat, 2013: 313; Endruweit, 2024: 109, fig. 216a) requires clarification. Nguyen VH & Nguyen HD (in Nguyen VH, 2006: 633, fig. 4) described *M. thacbaensis* from Vietnam:

Yen Bai Province: Yen Binh District: Thac Ba reservoir [21°51’N 104°58’E]. [It is noteworthy that the authors of the name are indicated as Hao & Duc [Nguyen VH & Nguyen HD] in text and as Duc, Hao & Van [Nguyen HD, Nguyen VH & Ngo SV] in the figure caption]. The type locality is in the Red River drainage. It was listed by Kottelat (2013: 313) as a possible synonym of *M. undulatus*. The holotype and paratypes are reported as lost (Endruweit, 2014: 157, 2024: 109). Endruweit (2024: 109, fig. 216b) designated a neotype for *M. thacbaensis* (ZMB 35101; type locality: Vietnam: Tuyen Quang Province: Son Duong District [21°42’N 105°24’E]: Pho Day River, in Lo River watershed), reasonably close to the original type locality. However, Endruweit did not explain why a neotype was needed (*Code*, art. 75.3, 75.3.1) and nothing in his text suggests ‘exceptional need’ of a neotype. The absence or loss of a holotype alone is not a justification for the designation of a neotype (*Code*, art. 75.2). Endruweit had identified *M. thacbaensis* as a junior synonym of his *M. ‘undulatus’*. With the name *M. undulatus* now not available for a species from China or Vietnam (see above), *M. thacbaensis* becomes the valid name for this species. Admittedly, the original description of *M. thacbaensis* is uninformative and the ‘figure’ conveys simply no information (Fig. 15a), but Endruweit unambiguously identified it as the same as his *M. ‘undulatus’* and no *Mastacembelus* species has been reported from that area that could be confused with *M. thacbaensis*. Therefore, this neotype designation is invalid.

Kottelat (2001b: fig. 158) shows two specimens misidentified as *M. armatus*. The upper illustration shows a specimen from Mong Cai (at the Chinese border, near the shores of Gulf of Tonkin; Fig. 15c). The lower one shows a specimen from the Song Gam watershed near Chiem Hoa (in Tuyen Quang Province; the same as the intended ‘neotype’ of Endruweit, 2024; Fig. 15b).

Mastacembelus liemphuensis Vu THN, Nguyen VH & Nguyen THT, 2020: 147 was described from Vietnam: Lao Cai Province: Van Ban, Liem Phu [22°00’N 104°19’E], in the Nam Chan watershed, a tributary of the Song Hong [Red

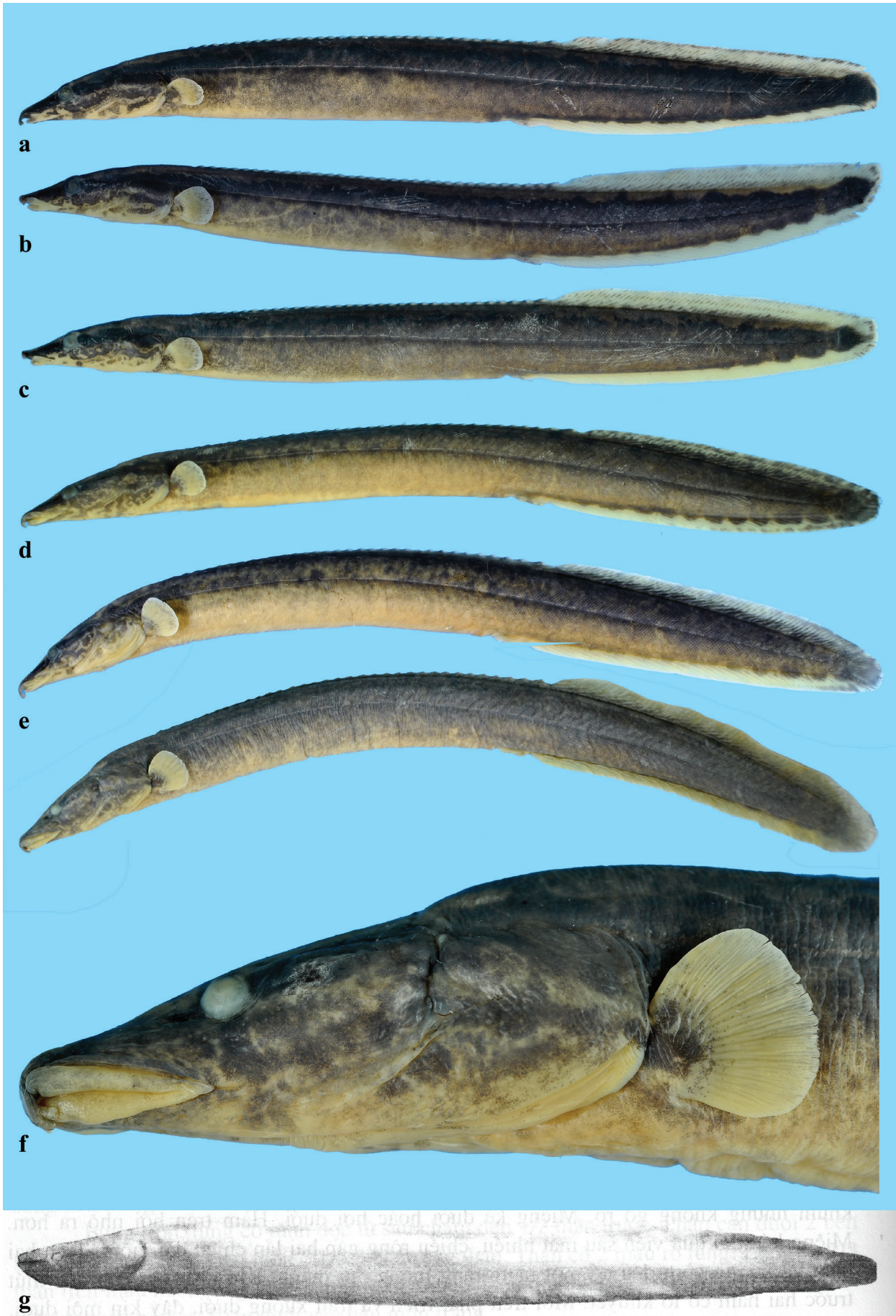


Fig. 18. *Mastacembelus dienbienensis*, a–f, CMK 20856; Laos: Nam Ou watershed: Houay Hut, near Phongsali; a, 81.6 mm SL; b, 84.6 mm SL; c, 87.9 mm SL; d, 117 mm SL (reversed); e, 123 mm SL; f, 261 mm SL (reversed); g, possibly holotype, 230 mm SL; Vietnam: Nam Ou watershed, Nam Nua (from original description, Nguyen, 2005: 632, fig. 3).

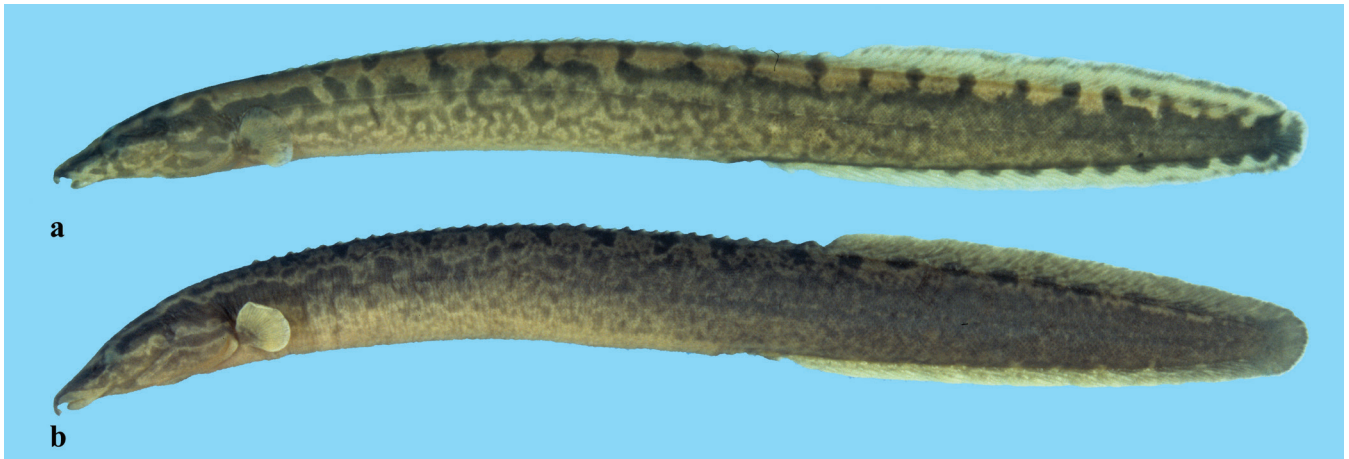


Fig. 19. *Mastacembelus dienbienensis*, CMK 21060; Laos: Nam Ou, downstream of Gnot Ou; a, 117 mm SL; b, 183 mm SL (reversed).

River]. Endruweit (2024: 112) considered *M. liemphuensis* as a synonym of *M. thacbaensis*.

Mastacembelus binhluensis Vu THN, Nguyen VH & Nguyen THT, 2020: 145 was described from Vietnam: Lai Chau Province: Tam Duong, Binh Lu [22°22'N 103°38'E; Nam Na watershed, tributary of the Song Da [Black River], itself a tributary of the Song Hong [Red River]]. Endruweit (2024: 113) explained that the type locality is Tac Tinh [22°20'51"N 103°36'49"E], a waterfall in Binh Lu commune, 2.5 km N of Tam Duong town. Endruweit (2024: 107, 112) tentatively treated it as a valid species and explicitly mentioned that it cannot be the same as his *M. undulatus* (here *M. thacbaensis*).

For *Mastacembelus liemphuensis* and *M. binhluensis*, the original descriptions do not allow a decision on their identity, let alone their validity. The two species are distinguished by the number of dorsal-fin spines (34–36 in *M. binhluensis* and 31–33 in *M. liemphuensis*), dorsal-fin rays (53–58, 61–63, respectively), anal-fin rays (53–55, 54–58, respectively) and caudal-fin shape. They do not appear to be members of the *M. armatus*-group. The material of *M. thacbaensis* that we examined had 34–36 dorsal-fin spines, 65–81 dorsal-fin rays, and 68–79 anal-fin rays. In the literature it was described as having 33–37, 63–78, and 64–80, respectively (Nguyen VH, 2006: 135, 633). Endruweit (2024: 109) reported 34–37, 63–77, 64–80, respectively.

Endruweit (2024: 107, 108) also described *M. pani* from the Gam watershed, a tributary of the Lo River, a northern tributary of the Red River; the type locality is in China but the river flows to Vietnam. He also described *M. truttoides* from the Nameguo He, a small northern tributary of the Red River, close to Vietnam. From the published information, both seem to be distinct and will not be discussed further here; also, they do not seem to belong to the *M. armatus* group.

The exact range of *M. thacbaensis* remains to be clarified. In Laos, *M. 'undulatus'* had been reported from the Nam Ma and Nam Neun drainages (Kottelat, unpublished reports). The Nam Ma becomes the Song Ma in Vietnam and enters the Gulf of Tonkin south of the estuary of the Red River. It is not connected to the Red River and the local *Mastacembelus*

might be *M. thacbaensis* or a distinct species (Fig. 16). The Nam Neun becomes the Song Ca in Vietnam and enters the Gulf of Tonkin at Vinh; again, the local *Mastacembelus* might be *M. thacbaensis* or a distinct species (Fig. 17). Considering the problems mentioned above with the literature on spiny eels of Vietnam and the limited material available, it is presently impossible to conclusively work on these fishes.

On the basis of the available data, the *M. 'undulatus'* of north-eastern Laos is identified as *M. thacbaensis*. This species differs from *M. dictyon* mainly by having the first dorsal-fin pterygiophore inserted behind the neural spine of the fifth vertebra (vs fourth). The stripe b is most conspicuous of all, more or less straight, usually boldest, wide, occupying most of the space between stripe c and the pale middorsal stripe, running until below the origin of the soft dorsal fin (e.g., Figs. 15c,d, 16b); in dark specimens with poorly contrasted colour pattern, stripe b covers most of the upper part of the flank, leaving only a narrow pale stripe between it and stripe c. Stripes c–e are thinner than stripe b, more or less linear anteriorly and very disorganised on the posterior third of the body. Bars of series I are often missing anteriorly; bars of series II–IV are irregularly organised, leaving blotches of series 1–3 irregular, often longitudinally elongated, angulous, sometimes with one or several black dots inside (e.g., Fig. 15c, 16b,d). The middorsal area is pale grey to yellowish, without complete transverse bands across the back. Dorsal, anal, and caudal fins have a wide hyaline or yellow margin. Specimens of *M. thacbaensis* that we observed in Laos frequently exhibit an irregular pattern, with the blotches of the series 1–4 often angulous or incomplete.

Identity of *Mastacembelus dienbienensis*. *Mastacembelus dienbienensis*, described by Nguyen & Nguyen (in Nguyen, 2006: 632, fig. 3), is a fourth nominal species described from northern Vietnam whose identity is not clear from the original description. It was listed by Kottelat (2013: 314) as a possible member of *Sinobdella*, of unknown validity. It was described from Dien Bien Phu in Dien Bien Province, in the Nam Nua and Nam Rom, in Mekong drainage. The holotype is reportedly lost (Endruweit, 2014b: 157). Dien Bien Phu is located in the Nam Nua watershed, a tributary of the Nam Ou, itself a main tributary of the Mekong flowing



Fig. 20. *Mastacembelus dienbienensis*, Laos: Nam Youan, CMK 25982. a, 113 mm SL; b, 139 mm SL (reversed).

almost entirely within Laos. The original description and the very poor illustration (Fig. 18g) do not allow identification of *M. dienbienensis* as any of the named *Mastacembelus* species known from the Lao section of the Nam Nua system (MK, pers. obs., 2010); the Nam Nua watershed, however, is still insufficiently surveyed (or at least the data have not been made public). At first sight, the absence of a proboscis in the figured specimen seems to exclude it as a species of *Mastacembelus*. It is reminiscent of *Sinobdella*, a genus unknown in the Mekong drainage but present in the Red River drainage. Consequently, Kottelat (2013: 314) only tentatively identified it as a species of *Sinobdella*. The Nam Nua is a tributary of the Nam Ou, itself a principal tributary of the Mekong. It originates in Vietnam, then forms the border between Vietnam and Laos (as the Nam Nua), finally entering Laos at about 21°14'49"N 102°49'17"E. The second author did limited sampling in the Nam Nua in 1997 and in 2009. The spiny eel collected in the Nam Nua closest to the Lao–Vietnam border was *M. dictyon*, about 2 km downriver of the border. These specimens have a colour pattern similar to that of specimens from the Nam Ngum (Figs. 7e,f); they have no similarity with the figure of *M. dienbienensis* in the original description. Two other species of *Mastacembelus* are present in the Nam Ou watershed in Laos. One of them has the general appearance of the specimen figured in the original description of *M. dienbienensis* (Fig. 18). In all specimens, the proboscis is very short (not quantified, but shorter than in most Asian congeners); in one specimen 261 mm SL (Fig. 18f), the proboscis is folded backwards against the lower jaw; this creates an appearance very similar to that of the specimen on the (extremely poor) illustration in the original description (here Fig. 18g). This specimen was collected in a small tributary of the Nam Ou

near Hatxa, about 80 river-km upriver of the confluence of the Nam Nua and Nam Ou. We identify this species as *M. dienbienensis*. Additional material was collected in the Nam Ou, downstream of Gnot Ou, about 150 river-km upstream of the confluence of the Nam Nua and Nam Ou (Fig. 19), in small tributaries of the Mekong near Hongsa (Xayaburi province), and in the Nam Youan (Louang Namtha Province: Muang Sing; Fig. 20). Examples of *M. dienbienensis* were later collected also near Louang Phabang (Praxaysombath et al., 2020; Nagao Natural Environment Foundation, 2020: 351; as *M. cf. pantherinus*). Since then, it has also been recorded from the Mekong drainage in the Luosuojiang watershed (Xishuangbanna, China) (Endruweit, 2024: 113). *Mastacembelus dienbienensis* and *M. dictyon* have been collected together in the Nam Ou downstream of Gnot Ou.

Mastacembelus dienbienensis can be distinguished from species of the *M. armatus* group by its colour pattern, which consists of a mottled body, yellowish belly, and a row of black blotches along the base of the dorsal and anal fins. The mottling becomes denser and the blotches less distinct with increasing size (compare Figs. 18 and 19). In specimens less than about 100–120 mm SL there is a paler middorsal band extending from the tip of the snout to the base of the soft dorsal fin, with 10–11 narrow transverse bands. The caudal part of the body is not tapering, the caudal-fin base is truncate and the caudal fin blunt (vs tapering body in *M. dictyon*). There are 33–35 abdominal vertebrae, 46–47 caudal vertebrae, 80–82 total vertebrae; the last dorsal-fin spine is inserted behind the neural spine of 37th to 39th vertebra. There are 33–35 dorsal-fin spines and a low number of 60–67 dorsal and 63–70 anal-fin rays (based on 3 specimens, CMK 25950, 25982). Endruweit (2024: 111, 113) recorded



Fig. 21. *Mastacembelus tinwini*, Laos; a, CMK 26018, 113 mm SL; Nam Ma; b, CMK 28018, 92.5 mm SL; Hongsa (reversed); c, CMK 28018, 110 mm SL; Hongsa; d, CMK 28018, 178 mm SL; Hongsa.

59–66 dorsal-fin rays, 60–69 anal-fin rays, 34–35 + 48–49 = 82–83 vertebrae, while the original description (Nguyen, 2006: 632) mentions 70–77 dorsal-fin rays and 53–70 anal-fin rays. The largest specimen observed in the field was 610 mm SL. *Mastacembelus dienbienensis* does not belong to the *M. armatus* group.

***Mastacembelus tinwini* in the Mekong drainage.**

Mastacembelus tinwini was originally described from the Salween and Sittaung drainages in Myanmar (Britz, 2007). It has since been observed in the Irrawaddy drainage and in Tenasserim in Myanmar, and in Peninsular Thailand at least as far south as Phuket Province and in the Chao Phraya drainage (MK, pers. obs. [specimens from Myanmar, see Fig. 6 and Britz, 2007: fig. 2, 3a,c; specimen from Chao Phraya, see Kottelat, 2001a: 148, fig. 143 bottom]; Khachonpisitsak, 2007: 125). In the Mekong drainage, we observed the species as early as 1985 in Fang (Chiangmai Province, Thailand), but misidentified it as *M. armatus*, and later in Laos in small tributaries of the Mekong near Hongsa (Xayaburi Province; Fig. 21b,d), the Nam Ma (Fig. 21a) and the Nam Ou. It was

later collected near Louang Phabang (Praxaysombath et al., 2020; Nagao Natural Environment Foundation, 2020: 351; as *M. cf. tinwini*).

Mastacembelus tinwini is distinguished from all other species of the genus by a unique colour pattern consisting of five regular and parallel black stripes (stripes b–f of our terminology) along the body, frequently expressed as series of interrupted lines or broken up into individual blotches, without bars of series I–IV (or only on the posterior part of the body) and a white margin to the soft-dorsal, anal, and caudal fins. It is further distinguished from other species in the *M. armatus* group by a count of 41–43 + 47–51 = 89–92 vertebrae (Britz, 2007).

Comparison material

Mastacembelus armatus: GANGES/BRAHMAPUTRA DRAINAGE, northern India: NRM 69592, neotype, 245mm SL; West Bengal, Calcutta. — NRM 40430, 1; Ganga River drainage: about 65 km NNE of Calcutta, Tumapao River close to Duma village, shore. — NRM 24789, 3; West Bengal, Calcutta.

M. aff. armatus: CMK 8791, 20; India: Kerala: Panamkulam, 26 km on Chalakudy–Valparai road. — CMK 9388, 1; India: Kerala: Cauvery drainage: 5 km from Vythiri on road to Calicut. — CMK 17668, 1; Pakistan: aquarium specimens exported from Karachi. — CMK 9400, 1; India: Tamil Nadu: Punnani River near Pollachi. — CMK 7217, 2; Sri Lanka: Kalu Ganga.

M. aff. armatus: IRRAWADDY AND SALWEEN DRAINAGES: CMK 25522, 21; Myanmar: Kachin: stream entering Mali Hka from east, upstream of Kang Mu Lon. — CMK 25568, 7; Myanmar: Kachin: Nam Lone Ka Kaung, a tributary of Mula River, entering it east of Mulashidi. — CMK 26503, 3; Myanmar: Kachin: Putao: confluence of Mula Chaung and Mali Hka. — CMK 27238, 2; Myanmar: Sagaing Region: Irrawaddy River, about 27 km North of Mandalay. — CMK 14728, 2; Thailand: Mae Hong Son Prov.: Nam Mae Yuam watershed.

Mastacembelus cf. dictyon: Thailand: CHAO PHRAYA DRAINAGE: CMK 5214, 2; 33.8–160 mm SL; Chiang Mai Prov.: Mae Nam Ping, 60 km north of Chiang Mai; 19°17'15"N 98°57'59"E. — CMK 14998, 6; Nan Prov.: Menam Nan in Wiang Sa, 26 km south of Nan on road to Phrae

Mastacembelus dienbienensis: Laos: MEKONG DRAINAGE: CMK 20856, 6; Phongsali Prov.: Houay Hut, 4 road-km north of Hatxa on road along Nam Ou. — CMK 21060, 2, 117–183 mm SL; Phongsali Prov.: Nam Ou, downstream of Gnot Ou, Haat Veune rapids. — CMK 25982, 2; Louang Namtha Prov.: Nam Youan upstream of Ban Sop-I. — CMK 27974, 1, 234 mm SL; Xayaburi Prov.: Nam Sing at Ban Pak Houay Ngang, about 33 km on road from Hongsa to Louang Phabang. — CMK 27986, 1, 201 mm SL; Xayaburi Prov.: Houay At at Ban Pak Houay Ngang. — CMK 28033, 4, 180–241 mm SL; Xayaburi Prov.: Nam Yone 5 km South of Ban Houy Chouang.

Mastacembelus favius: Thailand: CMK 4871, 1; Ayuttaya Prov.: Ayuttaya. — CMK 20188, 3; Chantaburi Prov.: Mae Nam Thap Nimid, km 18 on road 2405 from Ban Thung Khanan to Ban Swan Som; Tonle Sap drainage. Additional material: 21 specimens from 7 sites in Thailand, Malay Peninsula and Cambodia.

Malaysia: CMK 8453, 2; Pahang: Gambang, stream behind Hindu temple west of junction of road from Kuantan to Segamat with road from Kuantan to Kuala Lumpur.

M. manipurensis: CMK 26613, 2; India: Manipur: confluence of Chakpi and Dujang streams upstream of Chakpikarong.

M. pantherinus: Myanmar: Kachin State: NRM 55321, holotype; NRM 40968, NRM 47972, 12 paratypes; Lake Indawgyi: lower 300 m of Nant Yen Khan Chaung, affluent of Lake Indawgyi, little south of Lonton village. — NRM 40687, 3 paratypes; Lonton Village market on Lake Indawgyi. — NRM 41034, 1 paratype; Nant Yen Khan Chaung, affluent of Lake Indawgyi, upstream of road, near Lonton

village. — CMK 24226, 7; Kachin State: Lake Indawgyi, fish landing at Lonton.

Mastacembelus thacbaensis: Vietnam: CMK 14882, 5; Quang Ninh Prov.: river at 15 km on road from Tien Yen to Mong Cai. — CMK 14952, 1; Quang Ninh Prov.: Ba Che river 4 km upriver of Ba Che city. — ANSP 210057, 1 ("neotype" of *M. undulatus*); Ninh Binh Prov.: Hoa Lu Distr.; Red River Delta: Day River.

Laos: NAM MA DRAINAGE: CMK 25698, 1; Houaphan Prov.: Nam Ma near Ban Sop Bao; 20°42'41"N 104°23'01"E. — CMK 15396, 6; Houaphan Prov.: Nam Ma at Xiang Kho; 20°49'07"N 104°08'36"E.

Laos: NAM NEUN DRAINAGE: CMK 15284, 7; Xiangkhouang Prov.: Nam Mat about 1 km East of Ban Phathang; 19°36'33"N 103°42'10"E. — CMK 25820, 3; Houaphan Prov.: Nam Xam watershed: Nam La, tributary to Nam Xam, at Ban Phien Khoun; 19°52'47"N 104°45'27"E. — CMK 25873, 1; Houaphan Prov.: Nam Neun, about 2.5 km upstream of Ban Nam Neun; 20°02'13"N 103°41'49"E. — CMK 25908, 1; Houaphan Prov.: Nam Lem, a tributary of Nam Neun, entering it downstream of Ban Son Khua; 20°03'02"N 103°39'18"E. — CMK 28998, 1; Xiangkhouang Prov.: Nam Mat upstream of Ban Vieng Kham; 19°41'06"N 103°29'17"E. — CMK 29028, 7; Xiangkhouang Prov.: Nam Mat at irrigation dam, at confluence with Nam Thé, near Ban Mo; 19°36'32"N 103°33'37"E. Additional material: 15 specimens from 6 sites.

China: Guangxi: NRM 49681, 1; FUCHUAN JIANG DRAINAGE: bought from Zhongshan market in Zhongshan County town. — NRM 49682, 2; Liu Jiang drainage: bought from Dongcong market in Sanjiang County town. — NRM 49683, 1; Hongshui He drainage: bought from Anyang market in Du'an County town. — NRM 49684, 1; Zuo Jiang drainage: stream crossing road Xiangshui-Zhenxing, ca 3–4 km NW of Xiangshui Xiang, at Banlongjiang Cun. — CMK 25698, 1; Guanghi: Longzhou Co.: Dong Gui village, Shuikou town.

Mastacembelus tinwini: Myanmar: IRRAWADDY, SITTAUNG, SALWEEN AND TENASSERIM DRAINAGES: NRM 55468, holotype; NRM 48646, 12 paratypes; Salween drainage: Mon state: Thaton market. — BMNH 2007.1.10.1, USNM 385951, 4 paratypes; Salween drainage: Kayin state: Kawkareik. — CMK 19715, 6 paratypes; Kayin: stream 'Chon Son' between Kyondaw and Phadaw, about 20 km northwest of Payathouzu (at border with Thailand). — CMK 24857, 12; Tenasserim drainage: Khamaungthawe stream near lower Seikphyone village. — CMK 24928, 10; Tenasserim drainage: Myaekanbaw Chaung, tributary of Khamaungthawe. — CMK 24947, 12; Tenasserim drainage: Ban Chaung, upstream of Myittar. — CMK 26982, 3; Kachin: Irrawaddy drainage: Nant Sa Ri Chaung, East of Bhamo. — CMK 27468, 9; Shan State: Kee Kwae Chaung, tributary of Linn War Chaung, itself tributary of Paunglaung Chaung, Kee Kwae village. Additional material: 87 specimens from 27 sites in Myanmar and Thailand.

Thailand: CHAO PHRAYA AND MAE KHLONG DRAINAGES, MALAY PENINSULA: additional material: 43 specimens from 26 sites in Thailand and Malaysia.

MEKONG DRAINAGE: CMK 5217, 2; Thailand: Chiang Mai Prov.: Mae Nam Fang, 35 km south of Fang on road to Chiang Mai. — CMK 14029, 1; Laos: Louang Phabang Prov.: Nam Ou watershed: gorges of Houay Houn, about 3 km upstream of Ban Houay Lek. — CMK 16106, 1; Thailand: Chiang Rai Prov.: Nam Ngao where it enters Mekong mainstream, about 1 km downriver of Ban Chaem Pong. — CMK 26018, 1; Laos: Louang Namtha Prov.: Muang Long: Nam Ma drainage: Nam An, upstream of Ban Nam An, a tributary of Nam Ma. — CMK 28018, 8; Laos: Xayaburi Prov.: Hongsa Distr.: Houay Aen at Ban Kaeng Aen, about 500 m from confluence with Mekong, 19°49'14"N 101°23'34"E. Additional material: 17 specimens from 6 sites in Laos and Thailand.

ACKNOWLEDGEMENTS

RB is grateful to Oliver Crimmen and James Maclaine (Fish Group in BMNH), Sven Kullander, Eric Ahlander, Bo Delling (NRM), Laishram Kosygin (ZSI), Mark Sabaj, and Kyle Piller (ANSP) and Mario Richter (MTD), for information on specimens, radiographs, and photographs (Fig. 14b). Ritva Roesler drew the templates for the illustrations of the colour pattern terminology. The photograph in Fig. 14d was provided by Beta Maharatvaraj, Chennai. Most material of the new species was collected by MK as by-product of surveys for various hydropower and conservation projects between 1996 and 2024, with the assistance of numerous fisheries officers, company staff, fishermen, villagers, boat operators, drivers, etc. MK especially thanks Thavone Phommavong (LARReC, Living Aquatic Resources Research Center, Vientiane) for his valuable and continuous help and companionship in the field over the last 10 years.

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