

Catfishes of the Genus *Glyptothorax* (Siluriformes: Sisoridae) in the Mae Klong River Basin, Thailand, with Taxonomic Implications for Several Southeast Asian Species

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Five species of *Glyptothorax* are identified from the Mae Klong River basin in western Thailand, only one of which, *G. buehneri*, was previously reported from the basin; others are *G. lampris*, *G. longinema*, *G. platypogonides*, and *G. schmidtii*. The morphological differences delineating species of *Glyptothorax* in the Mae Klong were visualized using principal component analysis of data taken from 105 specimens, and the latitudinal range and number of river basins over which all occur were found to be greater than previously recognized. *Glyptothorax platypogonides*, recently thought to range only as far north as peninsular Thailand, occurs in the Mae Klong and Chao Phraya basins in western and northern Thailand. *Glyptothorax schmidtii*, thought to occur only as far north as the Tanintharyi River, Myanmar, was found to be much more wide-ranging, with the inclusion of populations in the Mae Klong, Chao Phraya, and Mekong River basins. *Glyptothorax longinema* was found to occur outside of China in lower portions of the Salween River basin and in the Mae Klong basin. The presence of *G. lampris* in the Chao Phraya is questioned and its southern distributional limit was extended to the Tapi River basin. Phylogenetic reconstruction of COI sequence data for 127 individuals from across Southeast Asia revealed strong BI and ML support for recognition of 14 species in Thailand and suggested deep-rooted clades that are discussed as corresponding broadly to body coloration. *Glyptothorax callopterus* was found to be genetically distinct from *G. fuscus* and is resurrected from synonymy. A key to all species of *Glyptothorax* in Thailand is provided.

GLYPTOTHORAX is the most diverse genus of sisorid catfishes, with 119 species presently recognized as valid (Fricke et al., 2022). It is named for and distinguished from all other catfish genera by the thoracic adhesive apparatus, a disk of finely pleated skin on the breast, with ridges and grooves parallel or oblique to the axis of the body. The genus is widespread and ranges geographically from the Euphrates and Tigris basins in Turkey (Çiçek et al., 2020) east to the Yangtze River in China (Jiang et al., 2011) and south to Borneo and Java (Ng and Kottelat, 2016), with multiple species often found in each river basin. Owing to its broad overall range, examinations and revisions of *Glyptothorax* taxonomy have focused on river basins or geographic regions, most recently the Sundaic Islands and Malay Peninsula (Ng and Kottelat, 2016), the headwaters of the major south-flowing rivers in Yunnan, China (Jiang et al., 2011, 2012), and Manipur, India (Vishwanath and Linthoin-gambi, 2007). Near the center of these recent reviews lies Thailand, from which Fowler (1934) and Smith (1945) originally described several species of *Glyptothorax*. With descriptions of new species and redescrptions supported by modern molecular techniques focused primarily on neighboring regions in the intervening years, the diversity of the genus in the rivers of Thailand, none more so than the Mae Klong, requires reevaluation.

The Mae Klong River is located entirely in western Thailand and drains southeastward to the Gulf of Thailand, but no specimens of *Glyptothorax* from the basin were examined by Fowler (1934) or Smith (1945). Indeed, the Mae Klong is situated on the periphery of some of the major collecting expeditions of the nineteenth and early twentieth

centuries—Bleeker (1855) in Indonesia, Blyth (1860) in Myanmar, and Hora (1923) in peninsular Thailand—each of which produced descriptions of new species of *Glyptothorax*. The Mae Klong basin constitutes its own, eponymous freshwater ecoregion (Abell et al., 2008); however, its ichthyofaunal composition is heavily influenced by its neighboring basins, chiefly the Salween and Chao Phraya Rivers, and the myriad smaller rivers of the Malay Peninsula.

Glyptothorax was first reported from the Mae Klong River by Yap in 2002, although no species were named. The genus was not known from the basin at the time of a 1989 checklist of fishes in the region (Kottelat, 1989). Tongnunui et al. (2016) reported three species from the basin but identified only two, *G. laosensis* and *G. major*. Vidthayanon (2017) listed only one species, *Glyptothorax* sp. 1, and Panitvong (2020) listed and provided photographs for two: *G. buehneri* and *G. cf. macromaculatus*. The objectives of the present study were to determine the number of species of *Glyptothorax* in the Mae Klong basin and to identify and provide a morphological description for each. Sequence data from the mitochondrial cytochrome oxidase subunit I (COI) gene and morphological data were used to compare specimens recently collected from the Mae Klong with specimens from other drainages, including from type localities of several described species of *Glyptothorax*. Four species not previously known to occur in the Mae Klong River are herein determined to inhabit its waters and a fifth species is confirmed from earlier reports. Multiple species of *Glyptothorax* are identified in river basins elsewhere in Thailand from which they had not previously been reported, and taxonomic changes are indicated for some species.

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MATERIALS AND METHODS

Sampling and specimen care.—Live fishes collected by the authors for this study were collected, imaged, and euthanized humanely according to University of Florida IACUC protocol 202110365_01. Specimens were collected with dip nets and seines, fixed in 10% formalin, and stored in 70% ethanol. Tissue samples for DNA extraction and analysis were taken from fins and preserved in 95% ethanol. Abbreviations for institutions from which specimens were examined and tissues extracted for DNA follow Sabaj (2020) and are ANSP—Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA; NIFI—National Inland Fisheries Institute, Bangkok, Thailand; UF—Florida Museum of Natural History, Gainesville, FL, USA; UMMZ—University of Michigan Museum of Zoology, Ann Arbor, MI, USA. Material examined is categorized, in descending order, by: country, drainage basin, province or state, and river of capture. Specimens for which morphological and meristic data were measured and analyzed are denoted by a dagger † in the material examined sections. Parenthetical numbers following meristic data indicate the number of specimens for which that count was observed, and an asterisk * indicates the count for the holotype, when examined.

Morphological data collection and analysis.—Measurements were taken with dial calipers to the nearest 0.1 mm. Morphometric data are expressed as percent of standard length (SL) or head length (HL). Measurements and counts were taken on the left side of specimens unless damaged or when barbels were uncooperative. Measurements and counts followed Ng and Kottelat (2013) with clarification as follows: standard length was measured from the tip of the snout to the middle of the base of the caudal fin; the dorsal-fin origin, for all relevant measurements, was considered to be a point at the center of the notch separating the dorsal spine from the nuchal plate elements; pectoral-fin spine length was measured from its origin to the tip of its most distal ossified component; and body depth at the dorsal-fin origin was taken as the vertical distance from the point described above to the midline of the ventral surface of the body. Insertion refers to the posterior point of a fin base. Thoracic adhesive apparatus length was measured along the ventral midline from the anterior point to the posterior point, and apparatus width was measured wherever greatest. Terminology for the thoracic adhesive apparatus followed Ng and Kottelat (2016). Anal-fin rays were counted beginning with the first branched ray; unbranched rays preceding the branched could not be reliably counted and are not provided; the ultimate ray was counted as a separate ray even if unbranched. Vertebral counts were made from computed tomography scans.

Following identification of the species in the Mae Klong, a sheared principal component analysis (PCA) was conducted to identify morphometric characters of greatest significance in differentiating species in the river basin and plotted in base R (R Core Team, 2018) following the directions of Bookstein et al. (1985) for SAS. Morphometric data from 105 specimens were log-transformed, and a covariance matrix was partitioned and centered by species and regressed on a factor correcting for size. No missing data were permitted; all individuals included in the analysis were measured for a complete set of characters. The second and third principal components were plotted to visualize differences in shape

between species uncorrelated to size of the specimens (Humphries et al., 1981).

Molecular data collection and analysis.—The mitochondrial cytochrome oxidase subunit I (COI) molecular dataset was comprised of 127 individuals, 61 of which were sequenced and uploaded to GenBank during the present study (Table 1), and the remainder were downloaded from GenBank. All downloaded sequence data belonged to vouchered specimens examined by authors of previous studies on *Glyptothorax* for which geographic coordinates were provided (Jiang et al., 2011, 2012; Ng et al., 2012; Singh et al., 2012 and supplemental material; Chen et al., 2015; Table 2). Sequence data for taxa restricted to India, Myanmar, and China served to provide topographic structure to the phylogeny presented herein but are otherwise unaddressed, with species named as in the aforementioned studies. Sequence data were generated from topotypic samples of *G. fuscus*, *G. siamensis*, and *G. trilineatus*, and from samples from the type locality drainages of *G. buechanani* and *G. platypogonides*. *Gagata gagata* (DQ508076) and *Bagarius lica* (OK077104) were included as outgroup sisorid taxa.

DNA was extracted from preserved tissue using a QIAamp DNA mini kit (QIAGEN Inc.). Polymerase chain reaction (PCR) was performed to isolate and amplify the COI gene using MyTaq Red DNA polymerase and buffer (Bioline Reagents Ltd.) and the “FISH-BCL” and “FISH-BCH” primers developed by Baldwin et al. (2009). Thermocycling was carried out under the following parameters: 1) initial denaturation at 95°C for 4 minutes; 2) denaturation at 94°C for 1 minute; 3) annealing at 52°C for 1 minute; 4) extension at 72°C for 1 minute, 30 seconds; 5) steps 2–4 repeated 34 times; and 6) final extension at 72°C for 7 minutes. Purification of the PCR product and bidirectional Sanger sequencing were completed by Eurofin Genomics.

Sequence chromatograms were assembled and edited in Geneious 8.1.9 and aligned in Mesquite 3.5 (Maddison and Maddison, 2018) using Clustal W 2.1 (Larkin et al., 2007). Partitions by codon position and models of nucleotide substitution were selected with PartitionFinder 2.1.1 (Lanfear et al., 2016) using linked branch lengths, the corrected Akaike information criterion, and the greedy algorithm (Lanfear et al., 2012). Each codon position was partitioned separately and employed the general time reversible (GTR) model of nucleotide substitution with gamma distribution (+G).

Bayesian inference (BI) analysis was conducted with MrBayes 3.2.6 (Ronquist et al., 2012) using two independent runs of four chains and 20 million generations, with sampling every 1000 generations and the first 25% discarded as burn-in. *Gagata gagata* (DQ508076) was designated the outgroup in the BI analysis. Convergence of the BI runs was diagnosed by low average standard deviation of split frequencies (3.242×10^{-3}), the potential scale reduction factor (1.000), and high estimated sample size (min. 1331). Maximum likelihood (ML) analysis was performed with RAxML 8.2.10 (Stamatakis, 2014) using complete random starting trees, the default rapid hill-climbing algorithm, and 100 independent tree searches, and bootstrapped with 500 replicates per the autoMRE convergence criterion. Partitioning and phylogenetic analyses were carried out on the University of Florida supercomputer (HiPerGator).

Table 1. Voucher specimen and tissue data for sequences generated by the present study and included in the molecular phylogeny. Locality data in Table 2 and material examined sections. GenSeq designations follow Chakrabarty et al. (2013), with genseq-3 sequences representing topotypic data.

Species	Voucher no.	Tissue no.	GenBank no.	GenSeq
<i>Glyptothorax buchanani</i>	UF 183357	2012-0318	OK077086	genseq-4
<i>G. buchanani</i>	UF 183373	2012-0331	OK077087	genseq-4
<i>G. buchanani</i>	UF 188334	ICH-00302	OK077098	genseq-4
<i>G. buchanani</i>	UF 188350	ICH-00311	OK077099	genseq-4
<i>G. buchanani</i>	UF 191340	ICH-01564	OK077103	genseq-4
<i>G. buchanani</i>	UF 191736	ICH-01782	OK077106	genseq-4
<i>G. buchanani</i>	UF 192025	ICH-02865	OK077134	genseq-4
<i>G. buchanani</i>	UF 237479	2015-0435	OK077130	genseq-4
<i>G. callopterus</i>	UF 183899	2012-0163	OK077091	genseq-4
<i>G. callopterus</i>	UF 236160	2012-0595	OK077126	genseq-4
<i>G. dorsalis</i>	UF 192232	ICH-02904	OK077118	genseq-4
<i>G. fuscus</i>	UF 235947	2014-0135	OK077124	genseq-4
<i>G. fuscus</i>	UF 235987	2014-0182	OK077125	genseq-3
<i>G. lampris</i>	UF 183323	2012-0148	OK077085	genseq-4
<i>G. lampris</i>	UF 192046	ICH-03022	OK077113	genseq-4
<i>G. lampris</i>	UF 192046	ICH-03024	OK077114	genseq-4
<i>G. lampris</i>	UF 192320	ICH-02664	OK077120	genseq-4
<i>G. lampris</i>	UF 237478	2015-0423	OK077129	genseq-4
<i>G. laosensis</i>	UF 172618	2008-0488	OK077083	genseq-4
<i>G. laosensis</i>	UF 185202	2012-0636	OK077093	genseq-4
<i>G. laosensis</i>	UF 190469	ICH-01280	OK077133	genseq-4
<i>G. longinema</i>	UF 183312	2012-0064	OK077084	genseq-4
<i>G. longinema</i>	UF 191465	ICH-01677	OK077105	genseq-4
<i>G. longinema</i>	UF 192152	ICH-02820	OK077115	genseq-4
<i>G. longinema</i>	UF 192343	ICH-03161	OK077121	genseq-4
<i>G. longinema</i>	UF 192385	ICH-02688	OK077135	genseq-4
<i>G. longinema</i>	UF 192473	ICH-02708	OK077122	genseq-4
<i>G. platypogonides</i>	UF 166620	2006-0600	OK077079	genseq-4
<i>G. platypogonides</i>	UF 183399	2012-0336	OK077088	genseq-4
<i>G. platypogonides</i>	UF 183399	2012-0345	OK077089	genseq-4
<i>G. platypogonides</i>	UF 188274	ICH-00100	OK077096	genseq-4
<i>G. platypogonides</i>	UF 188323	ICH-00129	OK077097	genseq-4
<i>G. platypogonides</i>	UF 191776	ICH-03037	OK077107	genseq-4
<i>G. platypogonides</i>	UF 191850	ICH-02912	OK077109	genseq-4
<i>G. platypogonides</i>	UF 191952	ICH-02965	OK077111	genseq-4
<i>G. platypogonides</i>	UF 192549	ICH-03021	OK077112	genseq-4
<i>G. platypogonides</i>	UF 237475	2015-0196	OK077128	genseq-4
<i>G. platypogonides</i>	UF 237587	2015-0422	OK077131	genseq-4
<i>G. aff. platypogonides</i>	UF 190437	ICH-01263	OK077101	genseq-4
<i>G. aff. platypogonides</i>	UF 190437	ICH-01265	OK077102	genseq-4
<i>G. aff. platypogonides</i>	UF 237477	2015-0119	OK077094	genseq-4
<i>G. robustus</i>	UF 161614	2005-0978	OK077076	genseq-4
<i>G. robustus</i>	UF 161617	2005-0972	OK077077	genseq-4
<i>G. robustus</i>	UF 166626	2006-0589	OK077078	genseq-4
<i>G. rugimentum</i>	UF 192225	ICH-02903	OK077117	genseq-4
<i>G. schmidtii</i>	UF 169840	2007-1117	OK077080	genseq-4
<i>G. schmidtii</i>	UF 169842	2007-1134	OK077081	genseq-4
<i>G. schmidtii</i>	UF 169842	2007-1143	OK077082	genseq-4
<i>G. schmidtii</i>	UF 181162	2011-0143	OK077132	genseq-4
<i>G. schmidtii</i>	UF 183903	2012-0172	OK077092	genseq-4
<i>G. schmidtii</i>	UF 188351	ICH-00310	OK077100	genseq-4
<i>G. schmidtii</i>	UF 191825	ICH-02928	OK077108	genseq-4
<i>G. schmidtii</i>	UF 191936	ICH-02873	OK077110	genseq-4
<i>G. schmidtii</i>	UF 192154	ICH-01005	OK077116	genseq-4
<i>G. schmidtii</i>	UF 192550	2012-0602	OK077127	genseq-4
<i>G. schmidtii</i>	UF 235944	2014-0137	OK077123	genseq-4
<i>G. trilineatus</i>	UMMZ 245972	—	OK077136	genseq-3
<i>G. aff. trilineatus</i>	UF 183898	2012-0098	OK077090	genseq-4
<i>G. aff. trilineatus</i>	UF 188260	ICH-00019	OK077095	genseq-4
<i>G. aff. trilineatus</i>	UF 192233	ICH-02905	OK077119	genseq-4
<i>Bagarius lica</i>	UF 191424	ICH-01719	OK077104	genseq-4

Table 2. Geographic data for sequences generated by the present study and included in the molecular phylogeny.

GenBank no.	River drainage	Province	Country	Latitude	Longitude
<i>G. buchanani</i>					
OK077086	Chao Phraya	Chiang Mai	Thailand	19.222°N	98.839°E
OK077087	Chao Phraya	Chiang Mai	Thailand	19.212°N	98.859°E
OK077098	Chao Phraya	Chiang Mai	Thailand	18.223°N	98.463°E
OK077099	Chao Phraya	Chiang Mai	Thailand	18.277°N	98.384°E
OK077103	Mae Klong	Kanchanaburi	Thailand	14.659°N	98.534°E
OK077106	Chao Phraya	Nan	Thailand	18.852°N	100.650°E
OK077134	Mae Klong	Tak	Thailand	15.989°N	98.874°E
OK077130	Mae Klong	Kanchanaburi	Thailand	14.759°N	98.647°E
<i>G. callopterus</i>					
OK077091	Tapi	Nakhon Si Thammarat	Thailand	8.432°N	99.786°E
OK077126	Golok	Kelantan	Malaysia	5.751°N	101.981°E
<i>G. dorsalis</i>					
OK077118	Salween	Tak	Thailand	16.806°N	98.743°E
<i>G. fuscus</i>					
OK077124	Trat	Trat	Thailand	12.468°N	102.616°E
OK077125	Chanthaburi	Chanthaburi	Thailand	12.526°N	102.176°E
<i>G. lampris</i>					
OK077085	Tapi	Nakhon Si Thammarat	Thailand	8.349°N	99.692°E
OK077113	Mae Klong	Kanchanaburi	Thailand	14.759°N	98.647°E
OK077114	Mae Klong	Kanchanaburi	Thailand	14.759°N	98.647°E
OK077120	Mae Klong	Kanchanaburi	Thailand	14.544°N	98.785°E
OK077129	Mae Klong	Kanchanaburi	Thailand	14.759°N	98.647°E
<i>G. laosensis</i>					
OK077083	Mekong	Ubon Ratchathani	Thailand	15.325°N	105.490°E
OK077093	Mekong	Ubon Ratchathani	Thailand	15.391°N	105.455°E
OK077133	Mekong	Stung Treng	Cambodia	13.423°N	105.950°E
<i>G. longinema</i>					
OK077084	Mae Klong	Kanchanaburi	Thailand	14.917°N	98.667°E
OK077105	Mae Klong	Kanchanaburi	Thailand	14.940°N	98.657°E
OK077115	Mae Klong	Tak	Thailand	15.873°N	98.846°E
OK077121	Salween	Tak	Thailand	17.495°N	98.004°E
OK077135	Mae Klong	Kanchanaburi	Thailand	15.211°N	98.855°E
OK077122	Mae Klong	Kanchanaburi	Thailand	15.271°N	98.840°E
<i>G. platypogonides</i>					
OK077079	Musi	South Sumatra	Indonesia	4.106°S	104.138°E
OK077088	Chao Phraya	Chiang Mai	Thailand	19.286°N	98.690°E
OK077089	Chao Phraya	Chiang Mai	Thailand	19.286°N	98.690°E
OK077096	Chao Phraya	Phrae	Thailand	18.252°N	100.179°E
OK077097	Chao Phraya	Sukhothai	Thailand	17.551°N	99.771°E
OK077107	Mae Klong	Kanchanaburi	Thailand	14.427°N	98.836°E
OK077109	Tapi	Surat Thani	Thailand	9.115°N	98.977°E
OK077111	Tapi	Surat Thani	Thailand	8.751°N	98.750°E
OK077112	Mae Klong	Kanchanaburi	Thailand	14.759°N	98.647°E
OK077128	Chao Phraya	Phitsanulok	Thailand	17.253°N	100.629°E
OK077131	Mae Klong	Kanchanaburi	Thailand	14.759°N	98.647°E
<i>G. aff. platypogonides</i>					
OK077101	Mekong	Stung Treng	Cambodia	13.610°N	106.092°E
OK077102	Mekong	Stung Treng	Cambodia	13.610°N	106.092°E
OK077094	Mekong	Chiang Mai	Thailand	20.060°N	99.362°E
<i>G. robustus</i>					
OK077076	Tulang Bawang	Lampung	Indonesia	4.870°S	104.649°E
OK077077	Seputih	Lampung	Indonesia	5.072°S	104.884°E
OK077078	Tulang Bawang	Lampung	Indonesia	4.757°S	104.555°E
<i>G. rugimentum</i>					
OK077117	Salween	Tak	Thailand	16.806°N	98.743°E
<i>G. schmidtii</i>					
OK077080	Trat	Chanthaburi	Thailand	12.719°N	102.389°E
OK077081	Tonlé Sap	Chanthaburi	Thailand	12.907°N	102.403°E
OK077082	Tonlé Sap	Chanthaburi	Thailand	12.907°N	102.403°E

Table 2. Continued.

GenBank no.	River drainage	Province	Country	Latitude	Longitude
OK077132	Pran Buri	Prachuap Khiri Khan	Thailand	12.533°N	99.450°E
OK077092	Pak Nakhon	Nakhon Si Thammarat	Thailand	8.432°N	99.786°E
OK077100	Chao Phraya	Chiang Mai	Thailand	18.277°N	98.384°E
OK077108	Tapi	Surat Thani	Thailand	9.151°N	98.951°E
OK077110	Mae Klong	Tak	Thailand	16.229°N	98.925°E
OK077116	Mae Klong	Tak	Thailand	15.873°N	98.846°E
OK077127	Golok	Kelantan	Malaysia	5.751°N	101.981°E
OK077123	Trat	Trat	Thailand	12.468°N	102.616°E
<i>G. trilineatus</i>					
OK077136	Sittang	Bago	Myanmar	—	—
<i>G. aff. trilineatus</i>					
OK077090	Phang Nga	Phang Nga	Thailand	8.571°N	98.490°E
OK077095	Salween	Mae Hong Son	Thailand	18.928°N	97.937°E
OK077119	Salween	Tak	Thailand	16.806°N	98.743°E
<i>B. lica</i>					
OK077104	Mae Klong	Kanchanaburi	Thailand	13.947°N	99.292°E

Evolutionary distance within and between identified species was estimated from averaging base differences per site over all sequence pairs in MEGA X (Kumar et al., 2018; Table 3).

Figure preparation.—Photographs of live and preserved specimens were taken with a Canon 7D camera and edited in Adobe Photoshop CC 2018. Maps were produced using ArcMap 10.5 in ArcGIS (Esri) with elevation data derived from Google Earth. Specimens included in the molecular phylogeny were plotted on maps with a filled circle, those examined morphologically but not included in the phylogeny with a ring, those from records in the literature and not examined with an X, and type localities with a star. The Nuijiang and Lancangjiang Rivers of China are referred to in the geographic labels on the phylogeny and in the text as the (upper) Salween and Mekong Rivers, respectively.

RESULTS

The Bayesian reconstruction is presented in Figure 1 with posterior probabilities and ML bootstrap support values

above and below the nodes, respectively. Five species were identified in the Mae Klong River basin: *G. buechanani*, *G. lampris*, *G. longinema*, *G. platypogonides*, and *G. schmidtii*. The topologies of the BI and ML trees were almost identical; in the latter analysis (not depicted), *Glyptothorax dorsalis* was recovered with moderate support as sister to all other clades in the polytomy in which it appears in Figure 1, and the clade containing *G. fucatus* and *G. zanaensis* was recovered with very low support as sister to that containing *G. lanceatus*, *G. longjiangensis*, and *G. ngapang*. In total, 30 species-level clades were resolved within *Glyptothorax* with strong support, with available names assignable to all but two, designated *G. aff. trilineatus* from the Salween River and *G. aff. platypogonides* from the Mekong River.

Of the five species revealed in the molecular phylogeny from the Mae Klong basin, *G. buechanani* was perhaps the easiest to resolve, owing to almost identical COI genes shared with sequences OK077098 and OK077099 from specimens collected near the type locality in the Mae Chaem tributary of the adjacent Chao Phraya River drainage (as well as readily discernable coloration). The within-group p-distance for all

Table 3. Mean inter- and intraspecific p-distances among all species of *Glyptothorax* occurring in Thailand and *G. trilineatus* from Myanmar, calculated from sequence data used to generate the molecular phylogeny in Figure 1 and given as percentages.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 <i>G. buechanani</i>	0.22														
2 <i>G. burmanicus</i>	9.84	0.31													
3 <i>G. callopterus</i>	11.12	9.86	0.41												
4 <i>G. dorsalis</i>	10.26	8.49	10.38	N/A											
5 <i>G. fuscus</i>	10.55	10.73	4.75	10.88	0.21										
6 <i>G. lampris</i>	8.20	11.62	12.48	10.95	12.06	0.98									
7 <i>G. laosensis</i>	9.37	8.84	10.74	6.73	10.03	10.61	1.42								
8 <i>G. longinema</i>	10.75	9.08	11.45	4.37	11.45	11.77	6.48	0.51							
9 <i>G. ngapang</i>	11.24	9.40	11.74	5.38	11.58	12.28	7.48	5.45	1.06						
10 <i>G. platypogonides</i>	10.39	12.53	13.67	12.02	13.35	10.96	11.04	12.33	12.71	1.46					
11 <i>G. aff. platypogonides</i>	10.48	12.41	13.17	12.14	14.13	10.40	12.04	12.27	12.90	6.38	1.30				
12 <i>G. rugimentum</i>	13.40	12.85	14.27	11.42	14.40	13.30	13.16	13.01	13.08	13.31	13.11	N/A			
13 <i>G. schmidtii</i>	9.68	9.06	10.34	6.26	9.53	10.70	3.13	6.45	6.88	12.17	12.82	13.77	0.76		
14 <i>G. trilineatus</i>	8.95	9.36	10.43	6.23	9.81	10.11	4.22	6.64	6.90	11.38	11.46	12.30	4.19	0.66	
15 <i>G. aff. trilineatus</i>	9.17	8.32	10.52	5.85	10.32	10.95	2.92	5.83	6.49	11.76	12.38	13.62	2.49	3.63	0.54

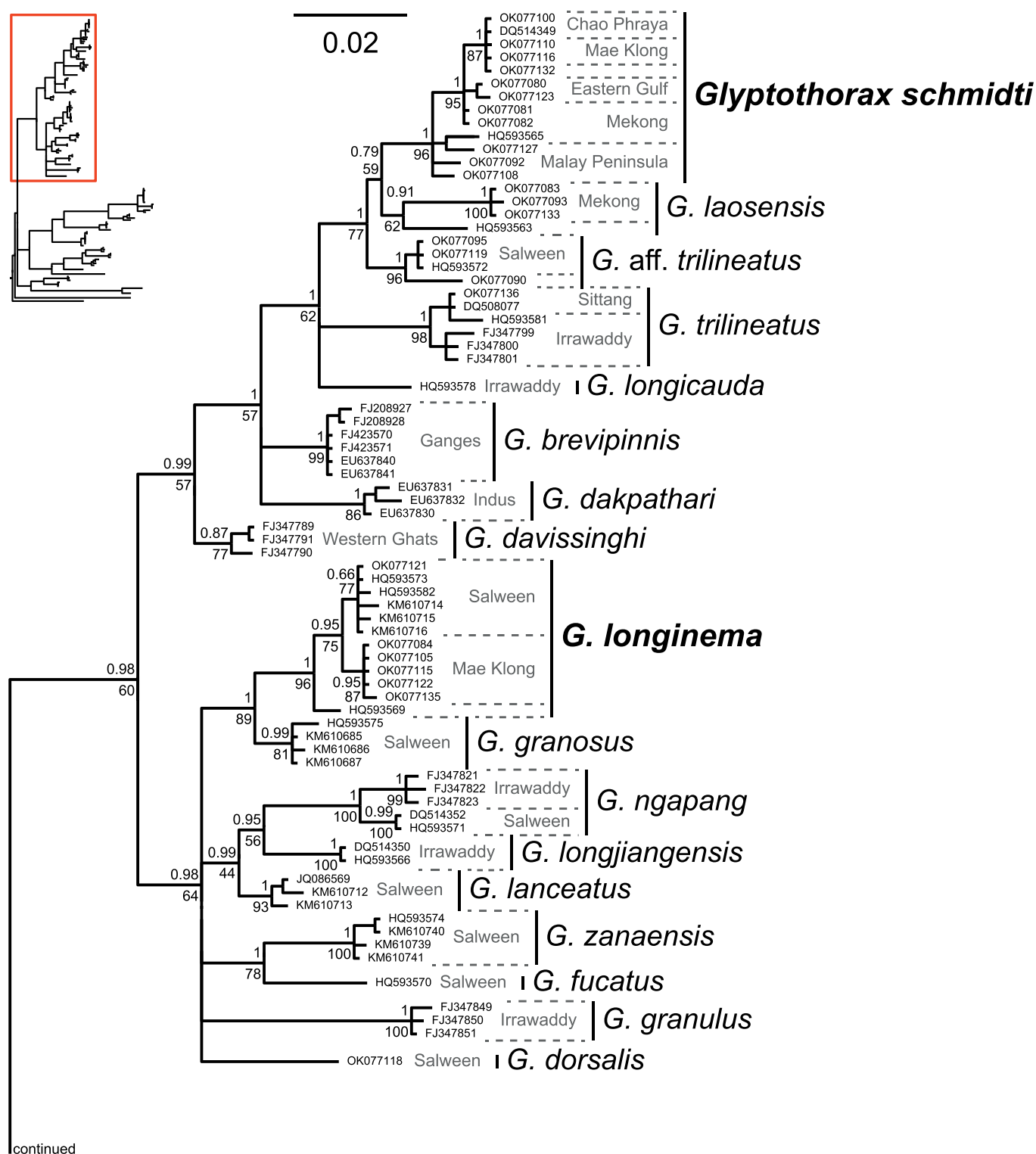


Fig. 1. Bayesian maximum clade credibility tree inferred from cytochrome oxidase subunit I (COI) gene for species of *Glyptothorax* and two outgroup sisorids. BI posterior probabilities plotted above nodes and ML bootstrap support values below. Species present in Mae Klong River in bold. Geographic distributions provided where shared by adjacent sequences. See Data Accessibility for tree file.

sequences of *G. buechanani* from both basins was a paltry 0.22% (Table 3).

The identification of *G. lampris* in the basin is based on morphology alone, as no genetic material was available from the type river basin. Fowler (1934) described *G. lampris* based on a single specimen from the Ping River, the largest tributary of the Chao Phraya River, in Chiang Mai, northern

Thailand. The holotype appears to remain the only voucher from the basin; no like specimen has been examined by the authors or reported from anywhere in the Chao Phraya. In 2012 and 2014, specimens matching Fowler's description were collected in the Tapi River in peninsular Thailand, and in 2015 and 2018 in the Mae Klong. This new material was compared morphologically to the holotype to confirm the

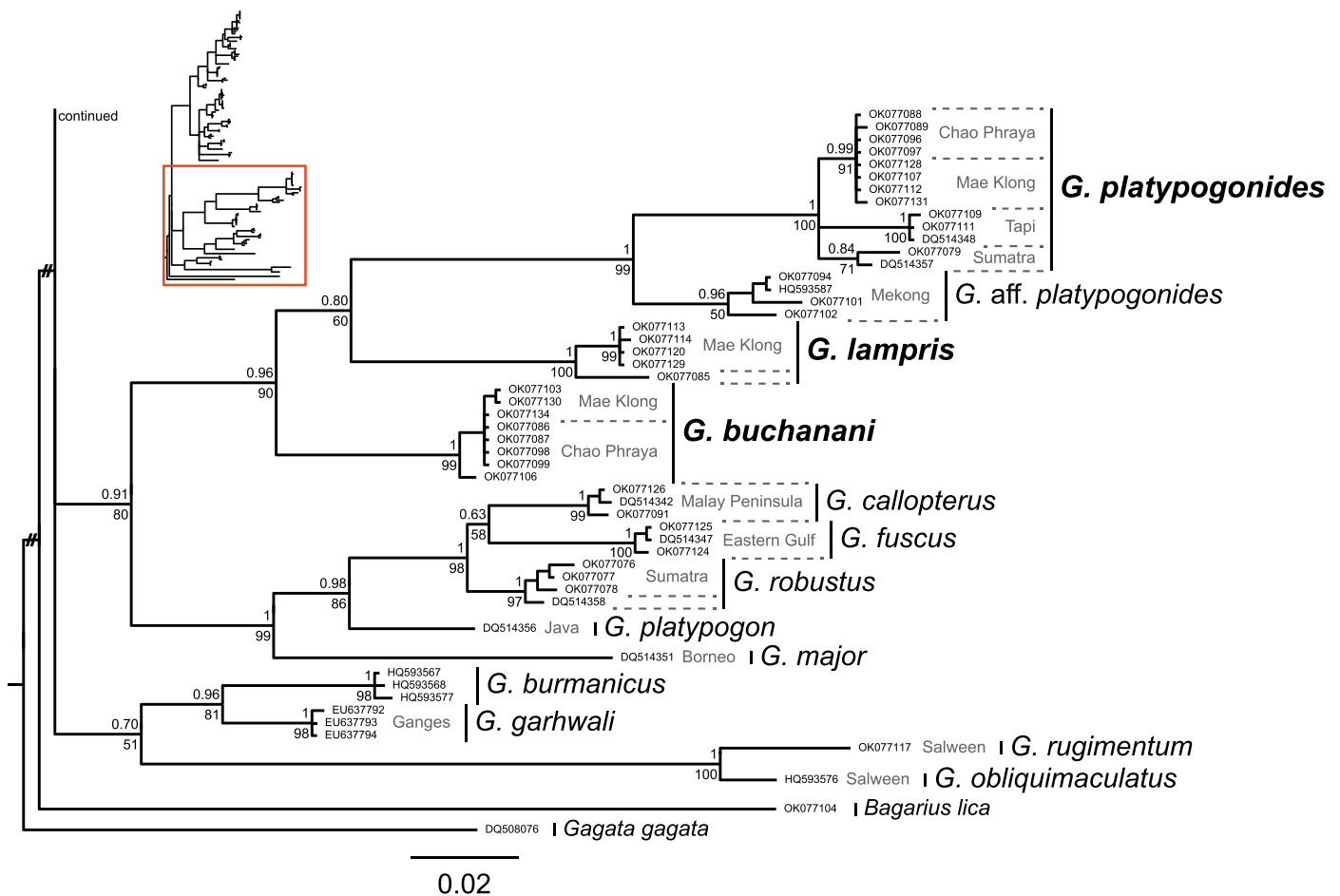


Fig. 1. Continued.

presence of *G. lampris* in those basins. The molecular analyses corroborate the close relationship of the Mae Klong and Tapi populations to one another (Fig. 1) with an intraspecific p-distance of 0.98% (Table 3). The status of *G. lampris* in the Chao Phraya is unknown. From the collections of de Schauensee, Fowler also received specimens from Nakhon Si Thammarat in the Malay Peninsula (through which runs the Tapi River), and it is not out of the question that he reported erroneous locality information for the *G. lampris* type. If not, the species is either extirpated from the Chao Phraya basin, or very rare. Certainly, it is not commonly collected anywhere across its known range.

Glyptothorax longinema, described from the upper Salween River in China, has not previously been reported from the Mae Klong and lower Salween Rivers or from anywhere in Thailand. The mitochondrial tree (Fig. 1) shows strong support for a clade containing novel sequences generated by the present study from the Mae Klong and Salween Rivers in Thailand and previously published sequence data from the upper Salween and Mekong Rivers in China (Jiang et al., 2011; Chen et al., 2015). The clade has an intraspecific p-distance of 0.51% (Table 3). The voucher specimens from this clade corresponding to the COI sequences with prefix "HQ," originally identified as *G. aff. zanaensis* (Jiang et al., 2011), were reidentified as *G. longinema* in a later morphological study and molecular analysis of cyt b and D-loop genes (Jiang et al., 2012). Sequence HQ593573 was taken from the vicinity of the type locality of *G. longinema* in Lushui,

Yunnan, and HQ593569 from that of its junior synonym, *G. rubermentus*, was collected in Baoshan, Yunnan.

Glyptothorax platypogonides, described from the Lematang River at Lahat in South Sumatra, was identified in the Mae Klong by the close phylogenetic relationship recovered between populations from both drainages, in addition to morphological comparison of Mae Klong specimens with topotypic material for which genetic data were unavailable. The specimen corresponding to sequence OK077079 was taken from a tributary of the Ogan River in East Baturaja, South Sumatra, which, like the Lematang, drains into the Musi River. While the populations of *G. platypogonides* in the Musi River in Sumatra, Tapi River in peninsular Thailand, and rivers of mainland Thailand are plainly visible in the phylogeny (Fig. 1) and separated by the greatest within-group p-distance among all species examined, that distance is only 1.46% among all basins (Table 3). The relationship among the populations is unresolved in a polytomy in the single-gene mitochondrial analysis. The mainland populations in the Mae Klong and Chao Phraya Rivers are genetically indistinct from one another (Fig. 1).

The fifth species in the Mae Klong River is *G. schmidtii*, described from northern Sumatra. As with *G. lampris*, genetic material was unavailable from the type locality. Ng and Kottelat (2016) examined specimens of *G. schmidtii* from Sumatra and concluded from morphological comparison that its range extends onto the Malay Peninsula. We follow their assumption and recognize the range of *G. schmidtii* to further

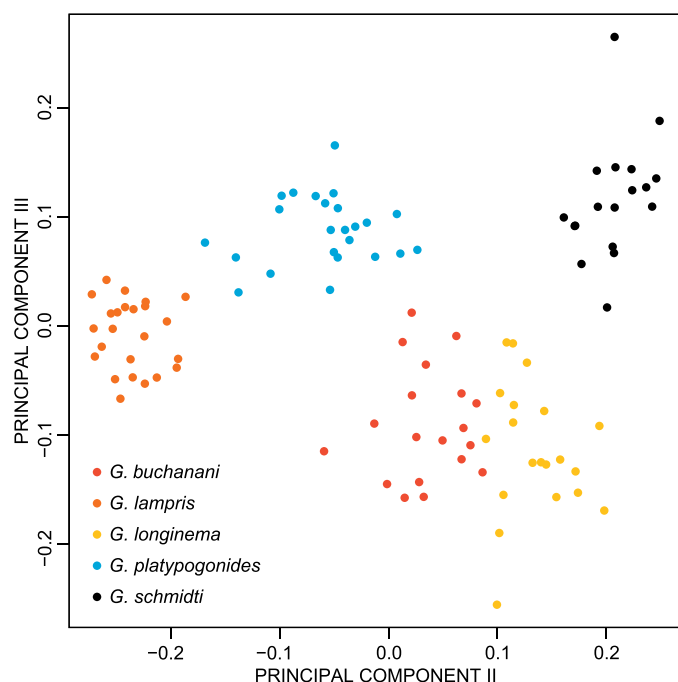


Fig. 2. Principal component analysis of Mae Klong species of *Glyptothorax*, corrected for size. Size (PCI, not plotted) accounted for 85.1% of observed variance, sheared PCII and PCIII for 6.4% and 2.5%, respectively.

include the Mae Klong, Chao Phraya, and eastern Gulf of Thailand drainages, as well as the Tonlé Sap in Cambodia, on the basis of the strongly supported clade formed between sequences from these localities and from a population in the Phum Duang (OK077108), Tha Di (OK077092), and Golok (OK077127) Rivers of peninsular Thailand and Malaysia—the population examined by Ng and Kottelat (2016). The within-group p-distance for all populations was 0.76% (Table 3), including one record (HQ593565) from the upper Mekong in China (Jiang et al., 2011). Sequence data from peninsular Thailand were taken from an area matching the type locality description of *G. siamensis* (OK077092) but did not indicate a second dark-bodied species present on the Malay Peninsula,

thus providing genetic support for placing *G. siamensis* in the synonymy of *G. schmidtii* as suggested by Ng and Kottelat (2016).

In the principal component analysis of morphometric data (Fig. 2), size (represented by the first principal component) accounted for 85.8% of observed variance and was not plotted. The sheared second and third principal components (PCII and PCIII) comprised 6.4% and 2.5% of observed variance, respectively, and are plotted in Figure 2. Those characters with the highest loadings on PCII were eye diameter (0.45), dorsal-to-adipose distance (−0.38), and dorsal-fin spine length (0.36). *Glyptothorax lampris* was separated from all other species along the PCII axis, as was *G. schmidtii* from all except *G. longinema*. Nasal-barbel length (0.53), post-adipose distance (−0.47), and adipose-fin base length (0.47) exerted the greatest influence on PCIII. On the PCIII axis, *G. platypogonides* is discrete from *G. buechanani* and *G. longinema*, and *G. longinema* is isolated from *G. schmidtii*.

The *Glyptothorax* of Southeast Asia have been categorized as either uniformly dark-bodied or irregularly colored with pale or dark bars (Ng and Kottelat, 2017). The molecular analysis finds phylogenetic support for clades corresponding to general body color (Fig. 1). A separate clade, containing *G. burmanicus* and relatives identifiable by complex thoracic adhesive apparatuses (Jiang et al., 2010), falls outside this categorization. The five species in the Mae Klong basin are members of the two clades defined by body color patterns. *Glyptothorax buechanani*, *G. lampris*, and *G. platypogonides* are broadly barred, while *G. longinema* and *G. schmidtii* are uniformly dark-colored with a pale, mid-lateral stripe. However, *G. buechanani* and *G. platypogonides* are highly variable and not always obviously barred. The two clades can also be separated by morphometric traits (Fig. 2), with the barred group having larger eyes, a shorter dorsal-to-adipose distance, and longer dorsal-fin spines.

Glyptothorax buechanani Smith, 1945

Figure 3

Glyptothorax buechanani Smith, 1945: 402, fig. 89 (type locality: Mae Tum [creek], Mae Chaem [river], Ping River drainage, northern Thailand).



Fig. 3. *Glyptothorax buechanani*, UF 191340, 39.9 mm SL; Thailand: Mae Klong basin: Pracham Mai River. Photo by Zachary Randall, Florida Museum of Natural History.

Table 4. Morphometric data for barred or irregularly colored species of *Glyptothorax* in the Mae Klong River.

	<i>G. buchanani</i> (n = 19)			<i>G. lampris</i> (n = 24)			<i>G. platypogonides</i> (n = 24)		
	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
Standard length (mm)		30.2–57.2			37.9–59.7			34.8–76.2	
% Standard length									
Predorsal length	38.3	35.8–41.0	1.31	40.2	38.5–42.0	0.94	37.5	35.9–39.9	0.93
Preal length	67.6	65.8–70.4	1.13	67.5	65.2–70.0	1.25	63.9	60.3–67.9	1.60
Prepelvic length	50.6	49.2–52.6	0.94	50.8	48.7–54.2	1.46	48.3	45.7–50.7	1.17
Prepectoral length	24.3	22.6–27.3	1.20	24.0	22.0–26.7	1.33	22.8	20.3–25.6	1.21
Dorsal-fin base length	14.8	13.7–15.7	0.55	14.4	13.3–15.4	0.55	13.2	12.1–14.3	0.52
Dorsal-fin spine length	19.1	16.8–21.0	1.05	21.0	18.8–22.8	1.11	18.9	16.4–20.8	1.08
Anal-fin base length	15.7	14.4–17.2	0.74	14.2	13.2–15.6	0.62	15.1	13.0–17.0	0.91
Pelvic fin length	17.8	16.6–19.0	0.63	15.8	13.7–17.6	0.93	15.5	13.9–17.0	0.84
Pectoral fin length	24.5	22.4–26.8	1.06	25.6	23.4–28.2	1.16	22.6	20.6–24.5	1.05
Pectoral-fin spine length	17.9	15.7–21.0	1.51	21.4	19.6–24.7	1.37	17.9	15.8–20.8	1.29
Caudal fin length	28.7	24.8–31.2	1.48	28.4	25.3–31.3	1.47	29.6	26.1–33.1	1.68
Adipose-fin base length	14.4	11.3–17.7	1.53	12.5	9.9–14.6	1.18	11.5	9.5–12.9	0.82
Dorsal to adipose distance	21.3	18.7–25.2	1.59	18.1	16.2–20.1	1.05	21.4	19.5–24.6	1.09
Post-adipose distance	17.0	15.1–18.4	0.88	18.6	17.1–20.0	0.79	20.9	19.1–22.3	0.89
Caudal peduncle length	17.6	15.9–19.1	0.88	19.2	17.6–20.5	0.85	21.4	19.4–22.5	0.75
Caudal peduncle depth	10.3	9.6–11.7	0.62	7.9	7.5–8.7	0.32	7.9	7.3–8.9	0.33
Body depth at anus	18.2	16.3–20.1	1.18	16.0	14.6–17.4	0.70	15.6	13.2–17.6	0.97
Body depth at dorsal-fin origin	21.8	19.0–24.8	1.65	21.4	18.6–24.2	1.41	20.0	16.4–21.6	1.25
Head length	28.2	26.6–29.7	0.96	28.4	26.0–29.9	0.95	26.9	25.4–29.5	0.97
Head width	23.2	21.6–24.2	0.73	22.7	21.1–24.8	0.96	20.5	18.6–22.1	0.89
Head depth	18.4	17.0–20.2	0.89	18.1	15.3–19.6	1.04	16.7	15.1–18.1	0.84
Adhesive apparatus length	16.2	14.0–20.8	1.53	17.1	14.3–19.2	1.29	16.8	14.4–18.4	1.16
Adhesive apparatus width	11.5	10.0–13.3	0.82	11.7	10.1–13.5	0.95	10.7	9.6–11.9	0.66
% Head length									
Snout length	49.0	45.9–52.5	1.45	49.1	45.9–50.8	1.21	49.3	45.0–52.7	1.63
Interorbital distance	29.9	27.9–31.8	1.40	27.2	22.7–29.9	1.60	25.6	23.0–29.0	1.46
Eye diameter	11.6	8.9–12.9	0.98	15.3	13.5–17.5	0.88	12.6	10.6–15.0	1.12
Nasal barbel length	21.9	16.5–24.8	2.24	20.4	17.5–24.2	1.73	20.4	17.1–24.9	2.18
Maxillary barbel length	86.0	74.6–95.8	5.60	101.6	88.5–113.6	6.87	88.5	76.2–99.0	6.72
Inner mandibular barbel length	27.6	24.2–31.9	1.91	38.4	34.8–45.0	2.54	32.2	26.0–37.7	3.40
Outer mandibular barbel length	43.1	38.6–47.8	2.39	56.9	50.7–63.3	3.39	50.4	43.3–60.0	4.18

Material examined.—Thailand: Chao Phraya drainage: Chiang Mai Province: Tang River: UF 183357, 1♂, 34.8 mm SL; UF 183373, 1♂, 35.0 mm SL. Mae Chaem River: UF 188334, 5♂ of 37, 30.2–52.4 mm SL; UF 188350, 3, 32.4–36.7 mm SL. Phitsanulok Province: Wang Thong River: UF 188423, 1, 38.6 mm SL. Nan Province: Senien River: UF 191736, 1♂, 37.6 mm SL. Mae Klong drainage: Kanchanaburi Province: Khayeng River: UF 181073, 4, 41.4–46.6 mm SL; UF 192371, 1, 39.6 mm SL. Prachin Buri River: UF 191340, 2♂, 37.8–39.9 mm SL. Malai River: UF 191451, 1, 37.0 mm SL. U Long Creek: UF 237479, 2♂, 38.1–46.5 mm SL. Song Karia River: UF 237481, 1, 40.0 mm SL. Ro Khi River: UF 245350, 3, 30.9–39.2 mm SL. Ran Ti River: UF 245502, 1, 38.7 mm SL. Tak Province: Khwae Yai River: UF 191934, 1, 46.4 mm SL; UF 192087, 3, 42.3–46.6 mm SL; UF 192097, 3, 41.5–57.2 mm SL. Umphang Creek: UF 192025, 2♂, 51.3–57.2 mm SL. Nong Luang Creek: UF 192130, 7, 32.3–40.3 mm SL. Mae Lamung Creek: UF 192171, 5♂ of 11, 39.5–49.9 mm SL.

Description.—Morphometric data in Table 4. Body deep, stocky, subcylindrical; from tip of snout, slightly convex and steeply inclined dorsally to deepest point at origin of dorsal fin, flat ventrally to origin of anal fin; slightly tapered thereafter to short, deep caudal peduncle. Anus closer to

origin of anal fin than to insertion of pelvic fin. Skin smooth. Lateral line complete; straight or softly arched; running from above gill opening midlaterally with slight dip at caudal peduncle and uptick at caudal base. Vertebrae 16+16–32 (1).

Head broad. Snout prominent. Anterior and posterior nares closer to tip of snout than to eye, separated by base of nasal barbel. Eye positioned dorsally, halfway along length of head. Gill opening broad, oblique. Mouth inferior, wide; upper lip thick and papillate; teeth small and villiform. Barbels in four pairs; nasal barbel slender, short, reaching halfway from base to eye; maxillary barbel fleshy at base, slender distally, reaching origin but not insertion of pectoral fin; mandibular barbels slender, short, outer barbel not reaching origin of pectoral fin.

Thoracic adhesive apparatus with striae arranged in elliptical disk extending posteriorly from isthmus but not reaching ventral midline parallel to insertion of pectoral fin; anteromedial striae absent; small posterior medial pit sometimes present (Fig. 4A).

Dorsal fin above anterior half of body; spine long; I,6 (19) rays; posterior margin straight; insertion halfway between tip of snout and base of caudal fin. Adipose fin closer to caudal base than to dorsal fin; anterior margin straight; pointed dorsally. Caudal fin forked, lobes equal in length; i,7,7,i (2) or

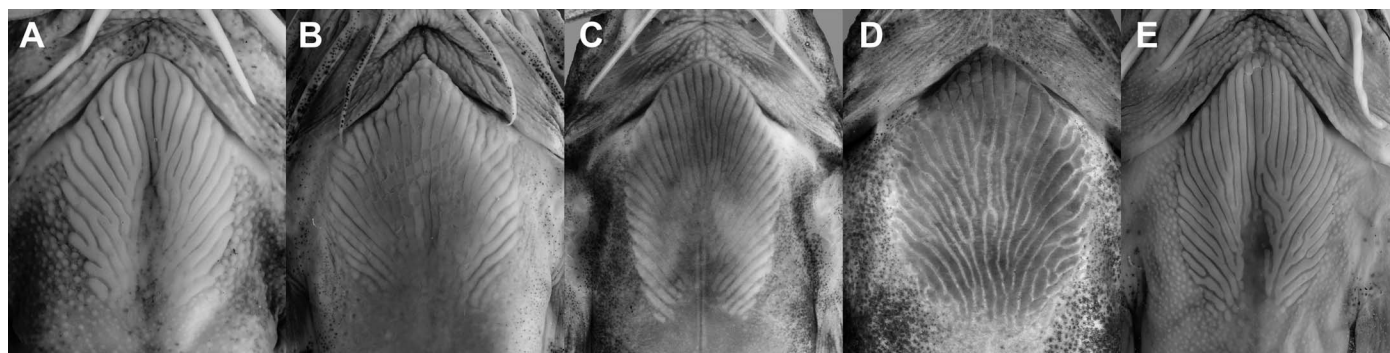


Fig. 4. Thoracic adhesive apparatuses of *Glyptothorax* in the Mae Klong River. (A) *G. buchanani*, UF 191340, 39.9 mm SL. (B) *G. lampris*, UF 237478, 59.7 mm SL. (C) *G. longinema*, UF 192385, 96.0 mm SL. (D) *G. platypogonides*, UF 245554, 74.7 mm SL. (E) *G. schmidtii*, UF 191936, 53.7 mm SL. Photos by Zachary Randall, Florida Museum of Natural History.

i,7,8,i (17) rays. Anal-fin origin slightly anterior to vertical through origin of adipose fin; 7 (1), 8 (5), 9 (10), or 10 (3) rays; posterior margin straight. Pelvic fin positioned ventrally, origin at vertical through insertion of dorsal fin; I,5 (19) rays. Pectoral fin situated ventro-laterally, parallel to plane of venter, origin immediately posterior to gill opening; spine with 7–13 serrations; I,8 (2), I,9 (16), or I,10 (1) rays.

Coloration.—In life, head very light to very dark brown above; anterior margin of upper lip and fleshy part of maxillary barbel gold; head and body light beige-gold ventrally. Body color highly variable, from light gold to dark brown, with three light to dark brown-gray bars below dorsal and adipose fins and on posterior half of caudal peduncle; bars inconspicuous or absent in very dark-colored individuals; many forms intermediate. All bars broad with poorly defined margins, darkest dorsally and faded ventrally. Bar below dorsal fin contiguous with brown coloration of head; posterior margin oblique, climbing from pectoral-fin base to beneath posterior extremity of dorsal-fin rays. Bar below adipose fin as wide as adipose-fin base length. Skin covering nuchal plate elements with striking, light gold saddle of variable width straddling dorsal-fin origin. Light gold middorsal stripe between dorsal and adipose fins, and between adipose and caudal fins. Light gold stripe along lateral line, narrow and inconspicuous in some individuals. All fins hyaline or translucent gold where not pigmented. Dorsal fin with dark brown base, spine, blotch at distal end of spine not reaching pale tip of fin, and narrow band separated from distal margin of fin membrane by hyaline margin; all pigment contiguous. Adipose fin dark brown with broad hyaline distal margin reaching insertion of fin. Caudal fin with brown to brown-gray chevron-shaped band at base; broad, chevron-shaped band at fork; translucent margin separating bands usually wide; tip of each lobe hyaline. Anal and paired ventral fins dark brown at base, with or without faint brown band near distal margin; pectoral spine brown. Preservation in alcohol has little effect on coloration.

Distribution.—Chao Phraya and Mae Klong River basins (Fig. 5).

Comparisons.—*Glyptothorax buchanani* is restricted to the Mae Klong and Chao Phraya Rivers and distinguished from all congeners in these basins, including close relatives *G. lampris* and *G. platypogonides*, by the light gold saddle of skin

covering its nuchal plate elements immediately anterior to the dorsal-fin origin (absent in all other species) and by the gold anterior margin of its upper lip. It further differs from *G. lampris* and *G. platypogonides* in having smooth (vs. rough) skin without prominent tubercles (vs. tubercles prominent), absent of irregular blotches or “mottling” (vs. skin mottled), by the position of the adipose fin closer to the caudal base than dorsal fin (vs. halfway between), and by the elliptical (vs. ovate) shape of the thoracic adhesive apparatus (Fig. 4); from *G. lampris* in having inconspicuous (vs. conspicuous) bars with nebulous (vs. well-defined) margins on a darker body, an adipose fin with a broad (vs. narrow) hyaline distal margin, a more gentle taper of the body from the origin of the dorsal fin to a deeper caudal peduncle (9.6–11.7% SL vs. 7.5–8.7), shorter inner (24–32% HL vs. 35–45) and outer (39–48% HL vs. 51–63) mandibular barbels, and straight (vs. concave) posterior margins of the dorsal and anal fins and anterior margin of the adipose fin; and from *G. platypogonides* in having a stockier overall appearance, with the dorsal profile rising more steeply from the snout to the origin of the dorsal fin, a shorter post-adipose distance (15.1–18.4% SL vs. 19.1–22.3), and a shorter (15.9–19.1% SL vs. 19.4–22.5), wider (9.6–11.7% SL vs. 7.3–8.9) caudal peduncle. In the Mae Klong River basin it is further distinguished from the uniformly dark-bodied species *G. longinema* and *G. schmidtii* by the dorsal profile rising more steeply from the snout to the origin of the dorsal fin and in having a longer dorsal-fin spine (16.8–21.0% SL vs. 11.1–16.4); from *G. longinema* by its gold (vs. much thinner, beige) midlateral stripe, predominantly translucent gold (vs. brown) fins, and shorter nasal barbel (16–25% HL vs. 26–37); and from *G. schmidtii* by the cessation of the midlateral stripe at the head (vs. its continuation to the eye), its longer prepelvic length (49.2–52.6% SL vs. 43.4–48.4) and dorsal-fin base (13.7–15.7% SL vs. 10.5–12.4), shorter post-adipose distance (15.1–18.4% SL vs. 18.6–23.4), and deeper head (17.0–20.2% SL vs. 13.0–16.4). It differs from *G. collopterus* and *G. fuscus* in southern and southeastern Thailand, respectively, by its light gold saddle; and from these as well as *G. ngapang*, the latter possessing similarly pale nuchal saddle elements and known from the Salween River, by the absence (vs. presence) of mottling on the head, body, and fins. It differs from *G. dorsalis*, known from the Salween River, by possession of a longer dorsal-fin base (13.7–15.7% SL vs. 10.1–12.1) and head (26.6–29.7% SL vs. 23.6–24.2) and a deeper caudal peduncle (9.6–11.7% SL vs. 6.6–6.8).

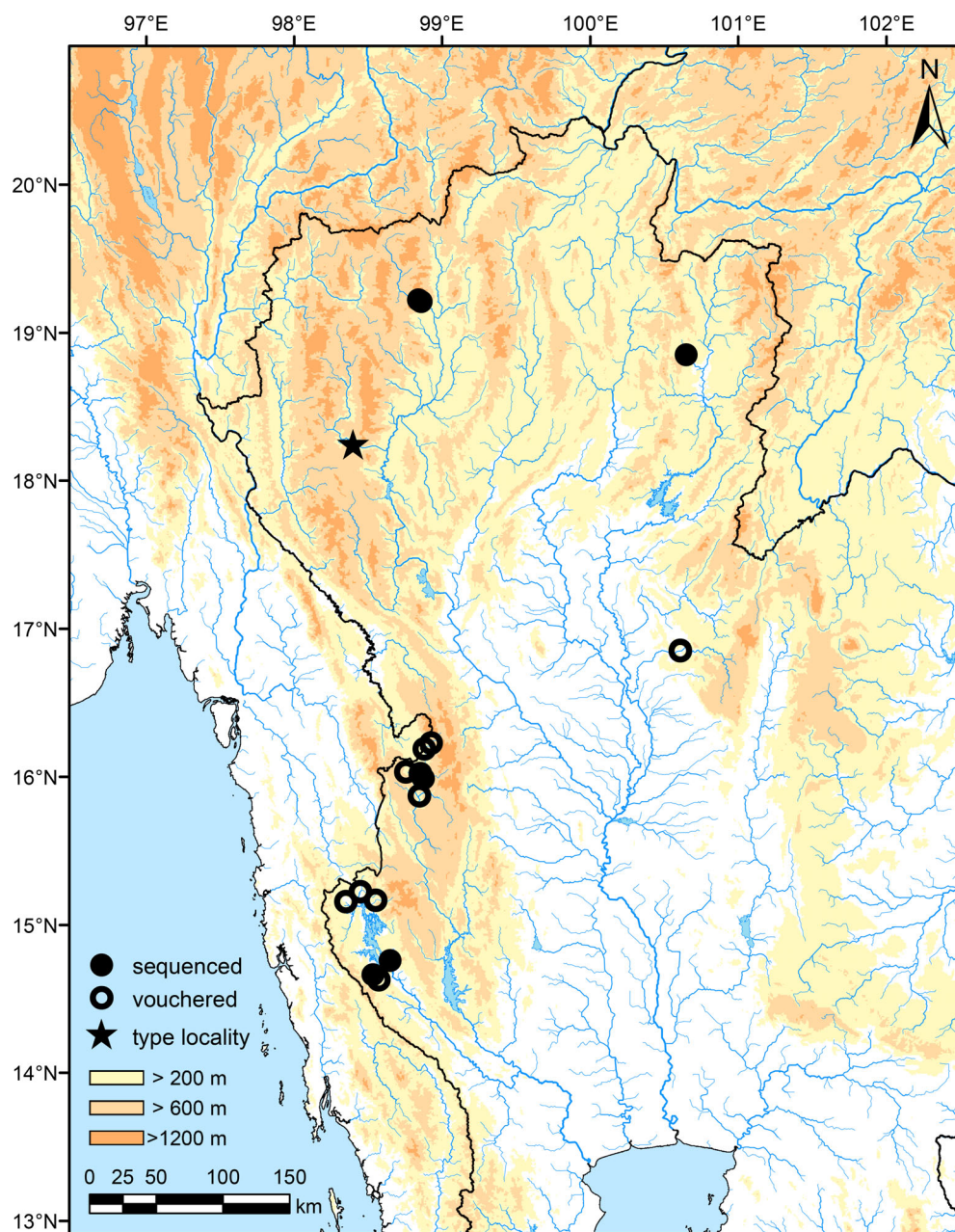


Fig. 5. Collection localities of *Glyptothorax buechanani*. COI sequence data from near type locality included in molecular phylogeny (OK077098–9).

Remarks.—Panitvong (2020) reported two species of *Glyptothorax* from the Mae Klong, *G. buechanani* (p. 490, top figure) and *G. cf. macromaculatus* (p. 486, top figure). Both photographs depict *G. buechanani*.

***Glyptothorax lampris* Fowler, 1934**

Figure 6

Glyptothorax lampris Fowler, 1934: 91, figs. 34–36 (type locality: Ping River, Chiang Mai, northern Thailand).

Material examined.—Thailand: Chao Phraya drainage: Chiang Mai Province: Ping River: ANSP 59357 (holotype), 42.7 mm SL. Mae Klong drainage: Kanchanaburi Province: Lin Thin River: UF 192320, 7♂ of 12, 39.1–53.7 mm SL. Mae Nam Noi Creek: UF 192046, 8♂, 37.9–46.2 mm SL; UF 192552, 1, 36.9 mm SL. U Long Creek: UF 237478, 5♂, 50.6–59.7 mm SL. Tapi drainage: Nakhon Si Thammarat: Tapi

River: UF 183323, 1♂, 44.3 mm SL; UF 236090, 3♂, 50.4–53.6 mm SL.

Description.—Morphometric data in Table 4. Body deep, stocky, subcylindrical; from tip of snout, slightly convex and steeply inclined dorsally to deepest point at origin of dorsal fin, flat ventrally to origin of anal fin; sharply tapered thereafter to short, slender caudal peduncle. Anus closer to origin of anal fin than to insertion of pelvic fin. Skin rough, covered in prominent tubercles of different sizes. Lateral line complete; straight or softly arched; running from above gill opening midlaterally with slight dip at caudal peduncle and uptick at caudal base. Vertebrae 16+18=34 (1) or 15+18=33* (1).

Head broad. Snout prominent. Anterior and posterior nares closer to tip of snout than to eye, separated by base of nasal barbel. Eye very large; positioned dorsally, halfway along length of head. Gill opening broad, oblique. Mouth inferior,



Fig. 6. *Glyptothorax lampris*. (A) UF 237478, 59.7 mm SL; Thailand: Mae Klong basin: U Long Creek. Photo by Zachary Randall, Florida Museum of Natural History. (B) ANSP 59357 (holotype), 42.7 mm SL; Thailand: Chao Phraya basin: Ping River. Photos by Kyle Luckenbill, Academy of Natural Sciences of Drexel University.

wide; upper lip thick and papillate; teeth small and villiform. Barbels in four pairs; nasal barbel slender, short, reaching halfway from base to eye; maxillary barbel fleshy at base, slender distally, very long, reaching insertion of pectoral fin; mandibular barbels slender, long, outer barbel reaching origin of pectoral fin.

Thoracic adhesive apparatus with striae arranged in ovate disk extending from isthmus to ventral midline parallel to insertion of pectoral fin; anteromedial striae absent; posterior medial pit absent (Fig. 4B).

Dorsal fin above anterior half of body; spine long; I,6* (25) rays; posterior margin concave; insertion halfway between tip of snout and base of caudal fin. Adipose fin about halfway

between dorsal fin and caudal base; anterior margin concave; pointed dorsally. Caudal fin forked, lobes equal in length; i,7,8,i* (25) rays. Anal-fin origin slightly anterior to vertical through origin of adipose fin; 8 (5), 9 (15), or 10* (5) rays; posterior margin concave. Pelvic fin positioned ventrally, origin at vertical through insertion of dorsal fin; I,5* (24) or I,6 (1) rays. Pectoral fin situated ventro-laterally, parallel to plane of venter, origin immediately posterior to gill opening; spine long, with 9–16 (holotype with 11) serrations; I,8* (25) rays.

Coloration.—In life, head brown-gold above; head and body light beige-gold ventrally. Body light gold to beige with three

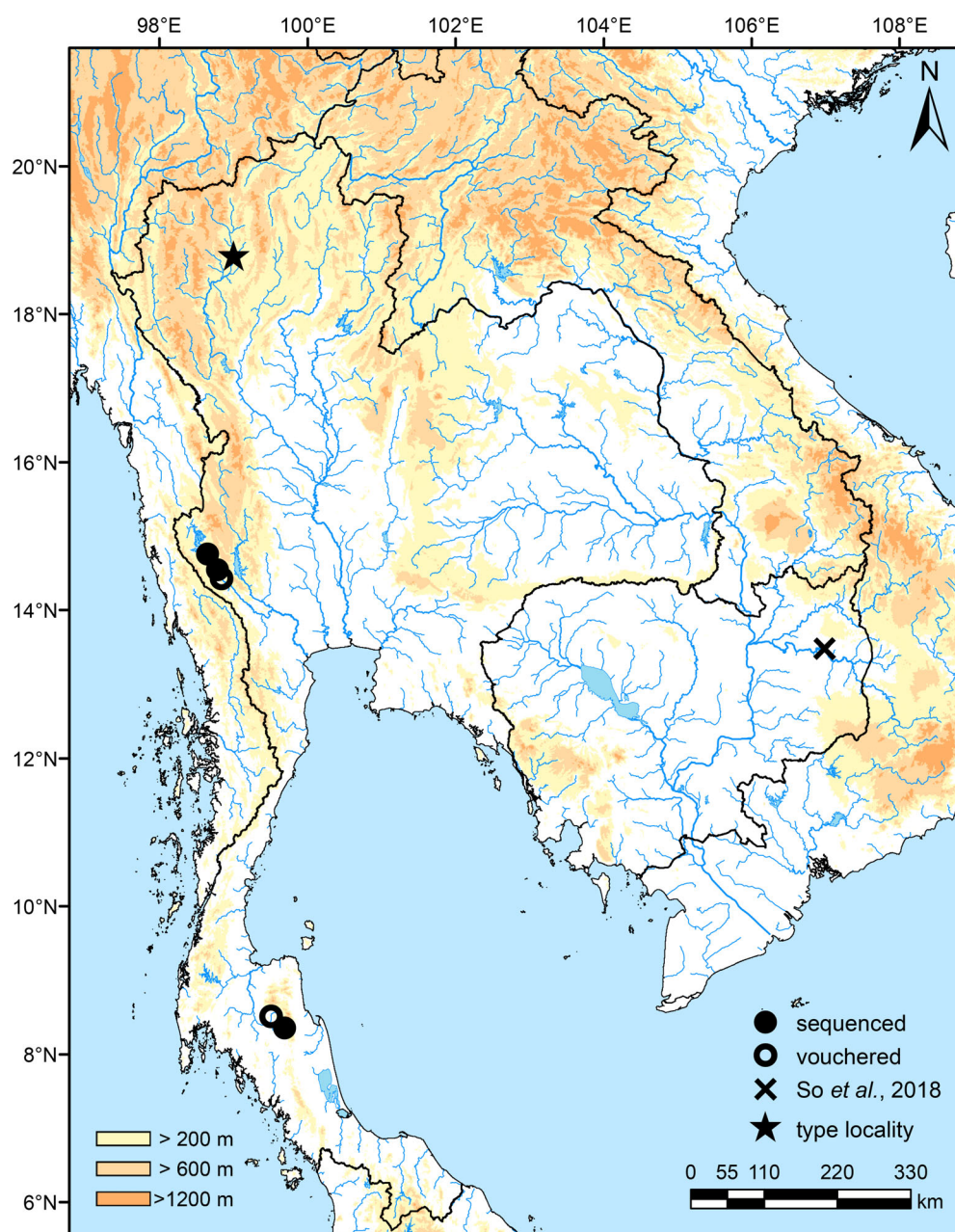


Fig. 7. Collection localities of *Glyptothorax lampris*. Cambodian record based on photograph in So et al. (2018; coordinates from N. So, pers. comm., 2021).

stark brown to brown-gray bars below dorsal and adipose fins and on posterior half of caudal peduncle. All bars broad with well-defined but jagged (or stair-like) margins. Bar below dorsal fin contiguous with brown-gold coloration of head; posterior margin oblique, climbing from pectoral-fin base to beneath posterior extremity of dorsal-fin rays. Bar below adipose fin as wide as adipose-fin base length above lateral line, often narrower below. Skin covering nuchal plate elements often slightly paler than adjacent tissue, conspicuous. Thin, light brown middorsal stripe between dorsal and adipose fins, absent in some individuals. Thin, gray stripe along lateral line, inconspicuous or absent in some individuals. Brown portions of head, body, fins, and margin of middorsal stripe mottled with small, dark, irregular blotches, only rarely present on pale, non-barred portions of body, absent entirely in some individuals. All fins hyaline or translucent gold where not pigmented. Dorsal fin with dark brown base, spine, blotch at distal end of spine not reaching

pale tip of fin, and broad band along distal margin of fin membrane; all pigment contiguous. Adipose fin dark brown with narrow hyaline distal margin. Caudal fin with light brown crescent- or chevron-shaped band at base; broad, irregular blotch on each lobe forming single, chevron-shaped band at fork of fin; translucent margin between bands usually wide; tip of each lobe hyaline. Anal and paired ventral fins light brown at base with brown band near distal margin; pectoral spine brown. Preservation in alcohol has little effect on coloration.

Distribution.—Chao Phraya, Mae Klong, Tapi, and Mekong River basins (Fig. 7). See remarks.

Comparisons.—*Glyptothorax lampris* is distinguished from all congeners by the well-defined, jagged edges clearly demarcating three broad, dark bars from its otherwise pale body (vs. bars inconspicuous, absent, or with nebulous margins). It

further differs from *G. platypogonides* in having a stockier overall appearance, with the dorsal profile rising more steeply from the snout to the origin of the dorsal fin and falling more steeply thereafter to the caudal peduncle; a longer maxillary barbel reaching the insertion (vs. origin) of the pectoral fin; and a longer outer mandibular barbel always (vs. rarely) reaching to the origin of the pectoral fin. From all other species of *Glyptothorax* in the Mae Klong and Tapi Rivers, *G. lampris* is distinguished by its rough (vs. smooth) skin covered in prominent tubercles of different sizes (vs. tubercles small, uniform size), the position of the adipose fin halfway between the dorsal fin and caudal base (vs. closer to caudal base), and by its large eye diameter (13–17% HL vs. 7–13). It further differs from *G. buechanani* by its more slender caudal peduncle (depth 7.5–8.7% SL vs. 9.6–11.7), longer inner (35–45% HL vs. 24–32) and outer (51–63% HL vs. 39–48) mandibular barbels, and concave (vs. straight) posterior margins of the dorsal and anal fins and anterior margin of the adipose fin; and from both *G. longinema* and *G. schmidtii* by the dorsal profile rising more steeply from the snout to the origin of the dorsal fin and falling more steeply thereafter to the caudal peduncle, possession of longer dorsal- (18.8–22.8% SL vs. 11.1–16.4) and pectoral- (19.6–24.7% SL vs. 12.7–18.0) fin spines, and the ovate (vs. elliptical) shape of the thoracic adhesive apparatus (Fig. 4). In the Tapi River, it is further distinguished from *G. callopterus* by having concave (vs. straight) posterior margins of the dorsal and anal fins and discrete (vs. indistinct) bands on the caudal fin. It differs from *Glyptothorax rugimentum*, which also has stark bars on a pale body, by the absence (vs. presence) of a fourth bar on the caudal peduncle and the cessation of adhesive striae at the isthmus (vs. adhesive striae extending onto the isthmus); *G. rugimentum* is only known from in and west of the Salween River drainage.

Remarks.—So et al. (2018: 115, middle figure) included a photograph labeled *G. fuscus* that appears to be of *G. lampris* from the Cambodian Mekong and indicated that the species represented is also present in the Thai and Lao stretches of the basin. Another photograph in that account, labeled *G. lampris* (p. 114, bottom figure), is not of *G. lampris*. Coordinates were provided for the locality (N. So, pers. comm., 2021) of the Cambodian specimen assignable to *G. lampris*, and the locality is included in Figure 7. Rainboth (1996: pl. 22) and Rainboth et al. (2012: pls. 40–41) included photographs of specimens identified as *G. lampris* from the Mekong River basin, but none is of *G. lampris*. Ng and Kottelat (2016) reidentified as *G. lampris* the photograph labeled *G. fuscus* in Kottelat (2001), but neither that photograph nor the one in Kottelat (2001) labeled as *G. lampris* are of *G. lampris*.

***Glyptothorax longinema* Li, 1984**

Figure 8

Glyptothorax longinema Li, 1984: 81, fig. 6 (type locality: Nujiang [Salween] drainage, Liuku, Yunnan, China).

Glyptothorax rubermentus Li, 1984: 83, fig. 8 (type locality: Lancangjiang [Mekong] drainage, Baoshan, Yunnan, China).

Material examined.—Thailand: Salween drainage: Mae Hong Son Province: Khong River: UF 190159, 2, 36.2–49.2 mm SL. Tak Province: Moei River: UF 192343, 5♂ of 6, 35.1–53.9 mm

SL. Mae Lamao River: UF 192553, 2, 30.8–33.8 mm SL. Ataran drainage: Mae Hong Son Province: Kasat River: UF 245438, 5♂ of 12, 39.2–83.1 mm SL. Mae Klong drainage: Tak Province: Mae Lamung Creek: UF 192152, 5, 40.8–57.6 mm SL. Kanchanaburi Province: Kroeng Krawia River: UF 183312, 7, 41.0–83.4 mm SL; UF 191465, 5♂, 42.5–84.1 mm SL. Song Thai River: UF 192385, 5♂ of 14, 39.2–96.0 mm SL. Dongwee River: UF 192473, 11, 24.0–75.7 mm SL. Talusa Creek: UF 192523, 10, 43.7–72.7 mm SL.

Description.—Morphometric data in Table 5. Body subcylindrical; from tip of snout, straight to slightly convex and gently inclined dorsally to deepest point at origin of dorsal fin, flat ventrally to origin of anal fin; slightly tapered thereafter to long caudal peduncle. Anus closer to origin of anal fin than to insertion of pelvic fin. Skin smooth. Lateral line complete; straight or softly arched; running from above gill opening midlaterally with slight dip at caudal peduncle and uptick at caudal base. Vertebrae 18+18–36 (1).

Head depressed. Snout prominent. Anterior and posterior nares closer to tip of snout than to eye, separated by base of nasal barbel. Eye small; positioned dorsally, halfway along length of head. Gill opening broad, oblique. Mouth inferior, wide; upper lip thick and papillate; teeth small and villiform. Barbels in four pairs; nasal barbel slender, very long, reaching to or almost to eye; maxillary barbel fleshy at base, slender distally, very long, reaching insertion of pectoral fin; mandibular barbels slender, outer barbel reaching origin of pectoral fin.

Thoracic adhesive apparatus with striae arranged in elliptical disk extending from isthmus past ventral midline parallel to insertion of pectoral fin; anteromedial striae absent; small posterior medial pit, absent in some individuals (Fig. 4C).

Dorsal fin above anterior third of body; spine short; I,6 (20) rays; posterior margin slightly concave; insertion halfway between tip of snout and base of caudal fin. Adipose fin closer to caudal base than to dorsal fin; anterior margin slightly concave; rounded. Caudal fin deeply forked, lobes equal in length; i,7,8,i (20) rays. Anal-fin origin slightly anterior to vertical through origin of adipose fin; 9 (8) or 10 (12) rays; posterior margin straight. Pelvic fin positioned ventrally, origin at vertical through insertion of dorsal fin; I,5 (20) rays. Pectoral fin situated ventro-laterally, parallel to plane of venter, origin immediately posterior to gill opening; spine short, with 7–14 serrations; I,9 (1), I,10 (16), or I,11 (3) rays.

Coloration.—In life, head and body uniformly brown to dark brown, light beige-gold ventrally. Thin, light brown middorsal stripe from tip of supraoccipital to caudal base. Skin covering nuchal plate elements often slightly paler than adjacent tissue. Tubercles along lateral line and skin between light beige, forming very thin stripe. Fins predominantly brown with hyaline distal tips and margins. Dorsal, anal, and paired ventral fins with faint, narrow to wide hyaline band halfway between base and distal margin. Preservation in alcohol has little effect on coloration.

Distribution.—Salween (including Ataran), Mae Klong, and upper Mekong River basins (Fig. 9).

Comparisons.—*Glyptothorax longinema* is distinguished from all congeners in the Mae Klong and lower Salween Rivers by its long nasal barbel (26–37% HL vs. 13–25) reaching



Fig. 8. *Glyptothorax longinema*, UF 192385, 96.0 mm SL; Thailand: Mae Klong basin: Song Thai River. Photos by Zachary Randall, Florida Museum of Natural History.

(vs. not reaching) the eye. It is further distinguished from *G. schmidtii* by its very thin, brown-beige (vs. thick, gold) middorsal and midlateral stripes, the latter originating above the gill opening (vs. at the eye). It further differs from *G. buechanani*, *G. lampris*, and *G. platypogonides* by the absence (vs. presence) of bars on its uniformly dark-colored body; from *G. buechanani* by its very thin, beige (vs. thicker, gold) midlateral stripe and predominantly brown (vs. translucent gold) fins, and shorter dorsal-fin spine (11.9–16.4% SL vs. 16.8–21.0); from *G. lampris* and *G. platypogonides* in having smooth (vs. rough) skin without prominent tubercles (vs. tubercles prominent), by the position of the adipose fin closer to the caudal base than to the dorsal fin (vs. halfway between), and by the elliptical (vs. ovate) shape of the thoracic adhesive apparatus (Fig. 4); and from *G. lampris* by possession of shorter dorsal- (11.9–16.4% SL vs. 18.8–22.8) and pectoral- (14.5–18.0% SL vs. 19.6–24.7) fin spines and a smaller eye diameter (7–11% HL vs. 13–17).

Remarks.—For a comprehensive morphological comparison of *G. longinema* to the uniformly dark-bodied congeners in

the upper Salween and Mekong Rivers, see Jiang et al. (2012).

***Glyptothorax platypogonides* (Bleeker, 1855)**

Figure 10

Pimelodus platypogonides Bleeker, 1855: 272 (type locality: Lahat, Sumatra).

Material examined.—Indonesia: Musi drainage: Sumatra (island): Ogan River: UF 166620, 7†, 34.8–50.1 mm SL. Lematang River: UF 166621, 9, 41.5–57.2 mm SL. Kikim Timur River: UF 166623, 1, 39.8 mm SL. Lintang River: UF 166625, 1, 49.5 mm SL. Thailand: Tapi drainage: Nakhon Si Thammarat Province: Tapi River: UF 236097, 5† of 11, 43.3–61.0 mm SL. Surat Thani Province: Yan River: UF 191850, 29, 31.0–64.9 mm SL. Phanom River: UF 191952, 2†, 66.0–76.2 mm SL. Mae Klong drainage: Kanchanaburi Province: Khae Laem dam: NIFI 01078, 4, 51.9–85.0 mm SL. U Long Creek: NIFI 03091, 3, 65.2–74.1 mm SL; UF 192549, 6† of 7, 52.7–67.5 mm SL; UF 237587, 3, 80.4–91.0 mm SL; UF 245554, 1, 74.7 mm SL. Kraban River: UF 191529, 3, 35.4–45.6 mm SL. Mae Nam Noi Creek: UF 191776, 12, 42.4–83.4 mm SL. Lin

Table 5. Morphometric data for uniformly dark-colored species of *Glyptothorax* in the Mae Klong River.

	<i>G. longinema</i> (n = 20)			<i>G. schmidtii</i> (n = 18)		
	Mean	Range	SD	Mean	Range	SD
Standard length (mm)		35.1–96.0			35.1–140.3	
% Standard length						
Predorsal length	35.8	33.2–39.0	1.64	35.5	32.7–37.4	1.14
Preanal length	64.9	62.3–68.1	1.38	64.7	60.2–66.9	1.82
Prepelvic length	47.7	45.7–49.9	1.31	46.6	43.4–48.4	1.30
Prepectoral length	21.6	18.7–25.4	1.56	21.4	19.4–23.1	1.11
Dorsal-fin base length	12.6	11.4–14.7	0.72	11.4	10.5–12.4	0.57
Dorsal-fin spine length	14.3	11.9–16.4	1.09	12.8	11.1–14.4	0.94
Anal-fin base length	15.0	14.1–16.9	0.63	15.0	13.2–16.7	0.98
Pelvic fin length	17.6	16.5–19.0	0.59	17.9	17.0–19.2	0.61
Pectoral fin length	23.9	22.0–25.7	0.87	21.9	20.0–24.9	1.28
Pectoral-fin spine length	16.3	14.5–18.0	0.97	14.6	12.7–17.8	1.41
Caudal fin length	28.1	25.0–31.5	1.31	27.7	26.4–29.2	0.83
Adipose-fin base length	15.2	12.4–17.6	1.42	11.2	8.2–14.0	1.58
Dorsal to adipose distance	23.9	20.9–27.5	1.94	24.9	20.6–28.2	2.41
Post-adipose distance	17.9	15.8–20.3	1.41	20.9	18.6–23.4	1.11
Caudal peduncle length	20.3	18.5–23.2	1.40	20.3	18.1–22.4	1.01
Caudal peduncle depth	8.6	7.2–10.1	0.94	8.4	7.1–9.6	0.66
Body depth at anus	15.1	13.3–17.2	1.13	14.7	12.5–17.1	1.12
Body depth at dorsal-fin origin	18.1	16.2–21.1	1.18	16.9	14.2–19.2	1.13
Head length	25.8	24.1–27.9	1.21	26.0	23.2–28.0	1.26
Head width	20.9	19.0–23.4	1.33	20.0	17.9–22.0	0.79
Head depth	15.3	13.1–17.1	1.13	14.7	13.0–16.4	1.01
Adhesive apparatus length	15.2	13.4–16.5	0.85	14.5	11.9–16.7	1.43
Adhesive apparatus width	10.6	9.2–11.6	0.68	9.8	8.9–10.7	0.56
% Head length						
Snout length	50.4	46.7–54.1	1.83	49.4	46.2–53.5	1.91
Interorbital distance	27.0	23.9–28.7	1.41	27.5	25.8–29.7	1.06
Eye diameter	9.6	7.3–11.2	1.06	9.9	6.8–10.9	1.04
Nasal barbel length	30.4	25.7–35.8	2.98	19.1	13.3–23.7	2.41
Maxillary barbel length	92.1	74.8–108.7	9.84	81.4	75.0–96.3	5.28
Inner mandibular barbel length	32.6	25.9–38.1	4.05	25.3	21.5–28.0	1.78
Outer mandibular barbel length	51.1	40.7–60.2	5.97	40.7	36.3–45.6	3.07

Thin River: UF 192555, 6, 43.4–56.4 mm SL. Phachi River: UF 237473, 2, 43.6–50.1 mm SL; UF 237476, 6, 38.1–59.1 mm SL. Taphoen River: UF 237474, 1, 46.9 mm SL. Chao Phraya drainage: Phitsanulok Province: Phak River: UF 237475, 2, 41.2–57.7 mm SL. Sukhothai Province: Yom River: UF 188323, 3, 33.0–42.8 mm SL. Phrae Province: Yom River: NIFI 04931, 2, 46.9–54.4 mm SL; UF 188274, 7, 36.2–69.2 mm SL. Phayao Province: Mae Chua Creek: NIFI 04924, 2, 49.6–67.5 mm SL. Chiang Mai Province: Ping River: UF 183399, 4†, 50.7–68.4 mm SL.

Description.—Morphometric data in Table 4. Body subcylindrical; from tip of snout, straight to slightly convex and gently inclined dorsally to deepest point at origin of dorsal fin, flat ventrally to origin of anal fin; slightly tapered thereafter to long, slender caudal peduncle. Anus closer to origin of anal fin than to insertion of pelvic fin. Skin rough, densely covered in prominent tubercles of different sizes. Lateral line complete; straight or softly arched; running from above gill opening midlaterally with slight dip at caudal peduncle and uptick at caudal base; with prominent tubercles. Vertebrae 16+18=34 (1).

Head depressed. Snout prominent. Anterior and posterior nares closer to tip of snout than to eye, separated by base of

nasal barbel. Eye large; positioned dorsally, halfway along length of head. Gill opening broad, oblique. Mouth inferior, wide; upper lip thick and papillate; teeth small and villiform. Barbels in four pairs; nasal barbel slender, short, reaching halfway from base to eye; maxillary barbel fleshy at base, slender distally, long, reaching origin but not insertion of pectoral fin; mandibular barbels slender, outer barbel not reaching origin of pectoral fin.

Thoracic adhesive apparatus with striae arranged in ovate disk extending from isthmus to or past ventral midline parallel to insertion of pectoral fin; anteromedial striae absent; small posterior medial pit sometimes present (Fig. 4D).

Dorsal fin above anterior half of body; spine long; I,6 (24) rays; posterior margin straight to concave; insertion halfway between tip of snout and base of caudal fin. Adipose fin about halfway between dorsal fin and caudal base; anterior margin straight to slightly concave; pointed dorsally. Caudal fin deeply forked, upper lobe sometimes greater in length than lower lobe; i,7,7,i (1) or i,7,8,i (23) rays. Anal-fin origin slightly anterior to vertical through origin of adipose fin; 8 (2), 9 (16), 10 (5), or 11 (1) rays; posterior margin straight to slightly concave. Pelvic fin positioned ventrally, origin at vertical through insertion of dorsal fin; I,5 (24) rays. Pectoral

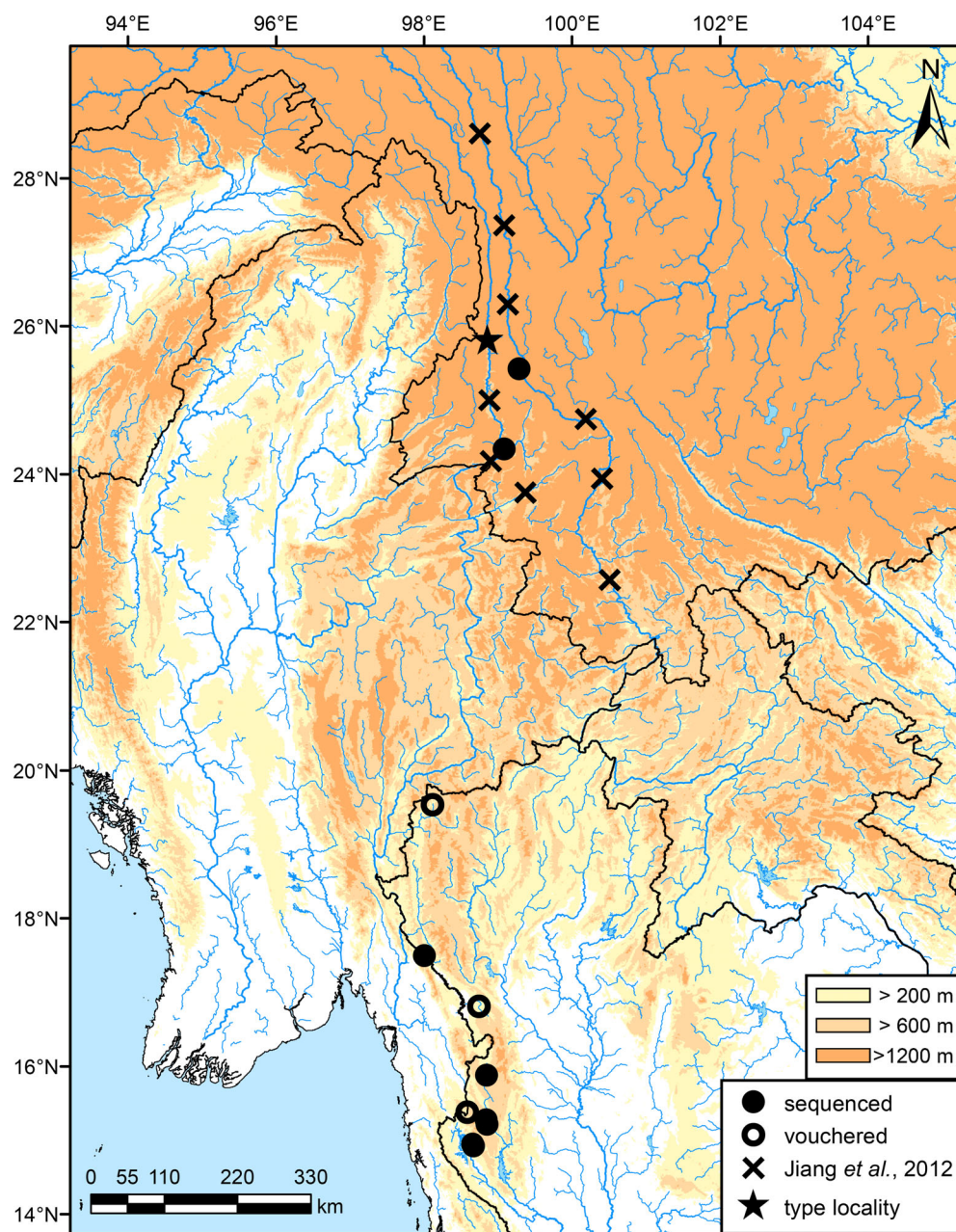


Fig. 9. Collection localities of *Glyptothorax longinema*. COI sequence data from type locality included in molecular phylogeny (HQ593573).

fin situated ventro-laterally, parallel to plane of venter, origin immediately posterior to gill opening; spine with 9–13 serrations; I,8 (4), I,9 (19), or I,10 (1) rays.

Coloration.—In life, head dark beige to dark brown above; head and body light beige-gold ventrally. Body color highly variable (see remarks), from light beige to gold to dark brown-gray, with three brown bars below dorsal and adipose fins and on posterior half of caudal peduncle; bars inconspicuous or absent or very dark-colored individuals; many forms intermediate. In barred form, bars below dorsal and anal fins broad with jagged margins. Bar below dorsal fin contiguous with dark beige or brown coloration of head; posterior margin oblique, climbing from pectoral-fin base to beneath posterior extremity of dorsal-fin rays. Bar below adipose fin as wide as adipose-fin base length. Skin covering nuchal plate elements with light beige to gold saddle straddling dorsal-fin origin; saddle inconspicuous or absent in some individuals.

Thin, light beige to gold middorsal stripe between dorsal and adipose, and between adipose and caudal fins. Tubercles along lateral line rimmed in light beige to gold, forming stripe, thin and inconspicuous in some individuals. Brown portions of head, body, and fins, and margins of middorsal stripe and lateral line mottled with small, dark, irregular blotches. Adipose fin brown with narrow to broad hyaline distal margin. Caudal fin with light to dark brown chevron-shaped band at base; broad, irregular blotch on each lobe sometimes forming single, chevron-shaped band at fork of fin separated from band at fin base by narrow or inconspicuous margin; sometimes disconnected at fork but independently contiguous with band at fin base; tip of each lobe hyaline. In uniformly dark brown-gray form, bars and mid-dorsal and -lateral stripes absent. Skin covering nuchal plate elements only slightly paler than adjacent tissue. Brown portions of head, body, and fins mottled with small, dark, irregular blotches. Adipose fin entirely dark brown-gray,



Fig. 10. *Glyptothorax platypogonides*. (A) UF 237476, 42.0 mm SL; Thailand: Mae Klong basin: Phachi River. (B) UF 245554, 74.7 mm SL; Thailand: Mae Klong basin: U Long Creek. Photos by Zachary Randall, Florida Museum of Natural History.

without hyaline margin. Caudal fin brown; tip of each lobe hyaline. In all forms, all fins hyaline or translucent beige-gold where not pigmented, with dark brown base; dorsal fin with brown blotch at distal end of spine not reaching pale tip of fin and broad brown band along or near distal margin of fin membrane; anal and paired ventral fins with or without light brown band near distal margin; dorsal and pectoral spines brown. Preservation in alcohol has little effect on coloration.

Distribution.—Southern and central Sumatra (Ng and Kottelat, 2016), eastern Malay Peninsula, and Mae Klong and Chao Phraya River basins (Fig. 11).

Comparisons.—*Glyptothorax platypogonides* is distinguished from *G. lampris* in having bars on the body with nebulous (vs. well-defined) margins or, rarely, no bars (vs. bars always present); an overall more slender appearance, with the dorsal profile rising more gently from the snout to the origin of the dorsal fin and falling more gently thereafter to the caudal peduncle; and a shorter maxillary barbel reaching to the origin but not insertion (vs. reaching insertion) of the pectoral fin. It is distinguished from all remaining congeners in the Mae Klong and across its range except *G. plectilis* in having rough (vs. smooth) skin covered in prominent tubercles of different sizes (vs. tubercles small, uniform size) and by the position of the adipose fin halfway between the dorsal fin and caudal base (vs. closer to caudal base). It further differs from *G. buechanani* in having an overall more slender appearance, with the dorsal profile rising more gently from the snout to the origin of the dorsal fin, a longer post-adipose distance (19.1–22.3% SL vs. 15.1–18.4), and a longer (19.4–

22.5% SL vs. 15.9–19.1), more slender caudal peduncle (depth 7.3–8.9% SL vs. 9.6–11.7). It differs from all uniformly dark-bodied congeners, including *G. longinema* and *G. schmidtii*, by the presence (vs. absence) of small, dark, irregular blotches on most of the head, body, and fins, and (except in unusually dark-bodied individuals of *G. platypogonides*) by the presence of three dark bars on its otherwise pale body (vs. bars absent, body uniformly dark). It is further distinguished from *G. longinema* and *G. schmidtii* by the pointed (vs. rounded) dorsal margin of adipose fin and ovate (vs. elliptical) shape of the thoracic adhesive apparatus (Fig. 4); from *G. longinema* by its predominantly translucent beige-gold (vs. brown) dorsal, anal, and paired ventral fins and shorter nasal barbel (17–25% HL vs. 26–37); and from *G. schmidtii* by its longer dorsal-fin spine (16.4–20.8% SL vs. 11.1–14.4). It differs from *G. plectilis*, which also has prominent tubercles of different sizes covering the skin, by the absence (vs. presence) of anteromedial striae on the thoracic adhesive apparatus (Fig. 4), and in having a shorter adipose-fin base (9.5–12.9% SL vs. 12.9–17.2) and longer post-adipose distance (19.1–22.3% SL vs. 14.0–17.6); *G. plectilis* is only known from Indian Ocean drainages of northern Sumatra.

Remarks.—*Glyptothorax platypogonides* has the most variation in body color and pattern among all species of *Glyptothorax* examined, although coloration remains a useful means of distinguishing it from its closest relatives, like *G. lampris*. Bleeker (1855) described greenish-violet skin with blue speckles, likely referring to iridescence from large tubercles, which he reported as covering the skin. Although specimens

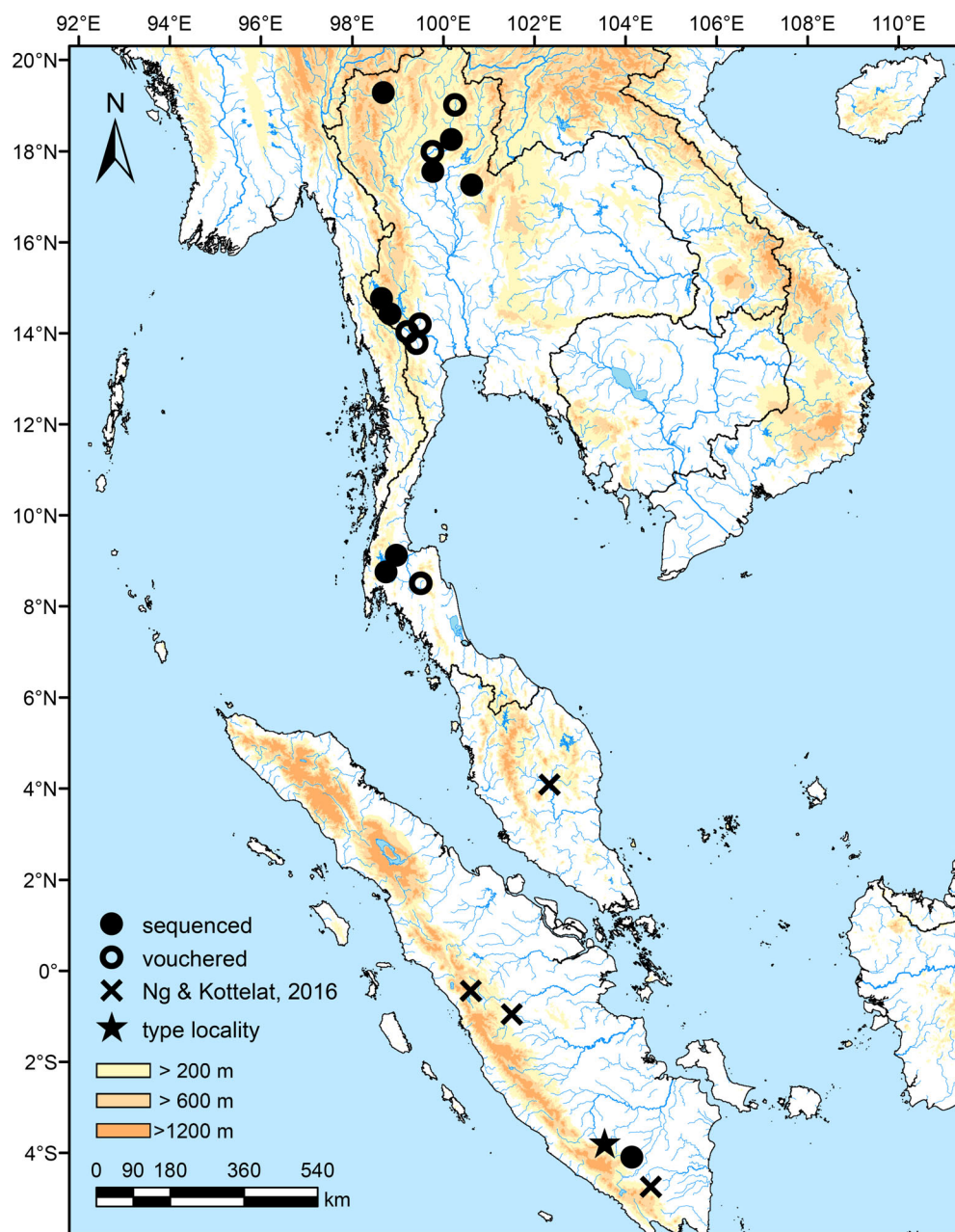


Fig. 11. Collection localities of *Glyptothorax platypogonides*.

with *G. lampris*-like coloration of the body (Fig. 10A) seem at odds with the type description and illustration of *G. platypogonides*, specimens at the other extreme with almost-uniformly dark brown-gray coloration of the body (Fig. 10B) align closely with Bleeker's account and Speigler's accompanying drawing (Bleeker et al., 2009: fig. 47). This may, in part, explain past confusion between *G. platypogonides* and *G. schmidti* (as *G. platypogonoides* [sic] and *G. siamensis* by Fowler [1934] and Smith [1945]) despite the present study finding little similarity between the two species.

***Glyptothorax schmidti* (Volz, 1904)**

Figure 12

Callomystax schmidti Volz, 1904: 470 (type locality: Dolok Simbolon [mountain], central Sumatra, Indonesia).

Glyptothorax siamensis Hora, 1923: 168, figs. 1–3 (type locality: Nakhon Si Thammarat hills, Thailand).

Material examined.—Malaysia: Golok drainage: Kelantan State: Golok River: UF 192550, 3♂, 37.9–40.1 mm SL. Thailand: Pak Phanang drainage: Nakhon Si Thammarat Province: Lan Saka Waterfall: NIFI 00501, 3, 43.5–113.3 mm SL. Tha Di River: UF 183903, 1♂, 35.1 mm SL. Tapi drainage: Nakhon Si Thammarat Province: Tapi River: UF 183908, 6, 40.7–80.2 mm SL. Surat Thani Province: Wae Creek: UF 191825, 7, 24.0–26.3 mm SL. Pran Buri drainage: Phrachuap Khiri Khan Province: Pala-U Waterfall: UF 181162, 1♂, 140.3 mm SL. Mae Klong drainage: Kanchanaburi Province: U Long Creek: NIFI 03092, 4, 47.9–57.2 mm SL; UF 245560, 2♂, 62.1–65.8 mm SL. Tak Province: Mae Lamung Creek: UF 192154, 2♂ of 3, 39.9–45.0 mm SL. Khwae Yai River: UF 191936, 4♂, 47.3–53.7 mm SL. Chao Phraya drainage: Chiang Mai Province: Mae Chaem River: UF 188351, 2♂, 42.8–48.2 mm SL. Trat drainage: Trat Province: Peed Creek: UF 235944, 5, 29.5–45.0 mm SL. Chanthaburi Province: Sato Noi Creek: UF 169840, 3♂, 70.0–86.6 mm SL. Tonlé Sap (Mekong) drainage:



Fig. 12. *Glyptothorax schmidtii*, UF 191936, 53.7 mm SL; Thailand: Mae Klong basin: Khwae Yai River. Photos by Zachary Randall, Florida Museum of Natural History.

Chanthaburi Province: Khruv Wui Creek: UF 169842, 7, 36.4–75.2 mm SL.

Description.—Morphometric data in Table 5. Body slender, subcylindrical; from tip of snout, straight to slightly convex and gently inclined dorsally to deepest point at origin of dorsal fin, flat ventrally to origin of anal fin; slightly tapered thereafter to long caudal peduncle. Anus closer to origin of anal fin than to insertion of pelvic fin. Skin smooth. Lateral line complete; straight or softly arched; running from above gill opening midlaterally with slight dip at caudal peduncle and uptick at caudal base. Vertebrae 18+18=36 (1).

Head depressed. Snout prominent. Anterior and posterior nares closer to tip of snout than to eye, separated by base of nasal barbel. Eye small; positioned dorsally, halfway along length of head. Gill opening broad, oblique. Mouth inferior, wide; upper lip thick and papillate; teeth small and villiform. Barbels in four pairs; nasal barbel slender, short, reaching halfway from base to eye; maxillary barbel fleshy at base, slender distally, not reaching insertion of pectoral fin; mandibular barbels slender, short, outer barbel not reaching origin of pectoral fin.

Thoracic adhesive apparatus with striae arranged in elliptical disk extending from isthmus to about ventral midline parallel to insertion of pectoral fin; anteromedial striae sometimes present; narrow, elongate posterior medial pit, absent in some individuals (Fig. 4E).

Dorsal fin above anterior third of body; spine short; I,6 (18) rays; posterior margin straight to slightly concave; insertion halfway between tip of snout and base of caudal fin. Adipose fin closer to caudal base than to dorsal fin; anterior margin slightly concave; rounded dorsally. Caudal fin deeply forked, lobes equal in length; i,7,8,i (18) rays. Anal-fin origin slightly anterior to vertical through origin of adipose fin; 8 (2), 9 (4), 10 (10), or 11 (2) rays; posterior margin slightly concave. Pelvic fin positioned ventrally, origin at vertical through insertion of dorsal fin; I,5 (18) rays. Pectoral fin situated ventro-laterally, parallel to plane of venter, origin immediately posterior to gill opening; spine short, with 7–15 serrations; I,9 (1) or I,10 (17) rays.

Coloration.—In life, head and body uniformly brown-gray to dark gray, light beige-gold ventrally. Thick, light beige to gold middorsal stripe from tip of supraoccipital to caudal base. Skin covering nuchal plate elements often slightly paler than adjacent tissue. Thick, light beige to gold midlateral stripe on head and body from eye to and along lateral line, very narrow or absent in some individuals (but always observed on specimens from the Mae Klong River). All fins hyaline or translucent gold where not pigmented. Dorsal fin with dark brown to dark gray base, spine, and blotch at distal end of spine not reaching pale tip of fin; all pigment contiguous. Adipose fin dark brown to dark gray with or without hyaline distal margin. Caudal fin predominantly brown, usually with hyaline distal tips; with faint chevron-shaped hyaline band

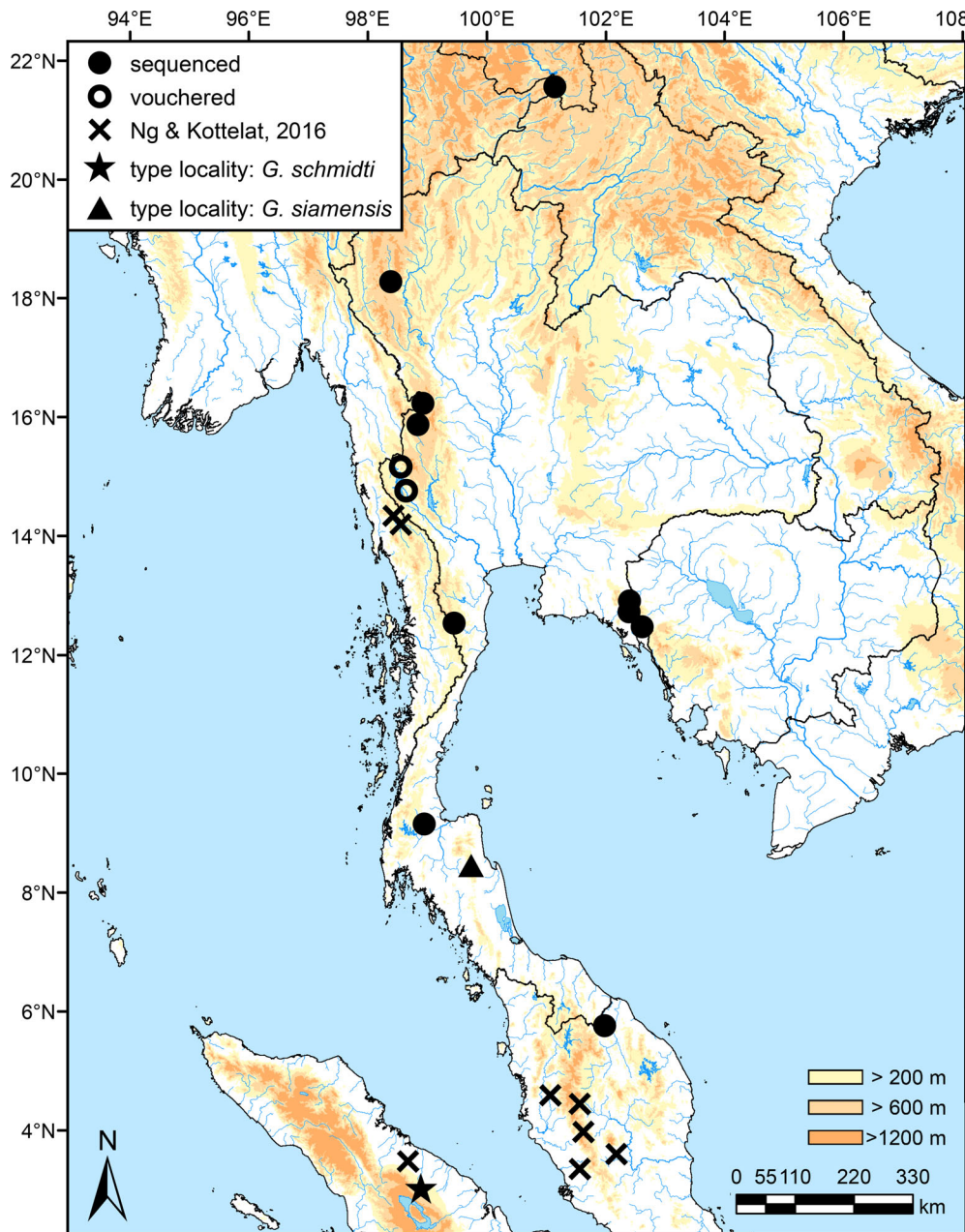


Fig. 13. Collection localities of *Glyptothorax schmidtii*. COI sequence data from type locality of *G. siamensis* included in molecular phylogeny (OK077092).

near base in some individuals. Anal and paired ventral fins with brown to gray blotch at base and blotch or band halfway between base and distal margin. Preservation in alcohol has little effect on coloration.

Distribution.—Northern Sumatra, Malay Peninsula, and scattered localities in mainland Southeast Asia, including the Tanintharyi River in Myanmar, Mae Klong, Chao Phraya, Trat, and Tonlé Sap (Mekong) River basins in Thailand, and the Mekong River in Yunnan, China (Fig. 13).

Comparisons.—*Glyptothorax schmidtii* is distinguished from all congeners in the Mae Klong except *G. longinema* by its uniformly dark-colored body without (vs. with) pale bars and from *G. longinema* by its usually thick, gold (vs. always very thin, brown-beige) middorsal and midlateral stripes, the latter originating at the eye (vs. above the gill opening). It

further differs from *G. longinema* by its shorter nasal barbel (13–24% HL vs. 26–37). It is further distinguished from the barred species *G. buechanani*, *G. lampris*, and *G. platypogonides* by its shorter dorsal-fin spine (11.1–14.4% SL vs. 16.4–22.8); from *G. buechanani* and *G. lampris* by in having a more slender overall appearance, with the dorsal profile rising more gently from the snout to the origin of the dorsal fin, and by its shorter dorsal-fin base (10.5–12.4% SL vs. 13.3–15.7); from *G. lampris* and *G. platypogonides* in having smooth (vs. rough) skin without prominent tubercles (vs. tubercles prominent) and absent of irregular blotches or mottling (vs. skin mottled), by the position of the adipose fin closer to the caudal base than dorsal fin (vs. halfway between), and by the elliptical (vs. ovate) shape of the thoracic adhesive apparatus (Fig. 4); from *G. buechanani* by the continuation of the midlateral stripe to the eye (vs. its cessation at the head), its shorter prepelvic length (43.4–48.4% SL vs. 49.2–52.6),

longer post-adipose distance (18.6–23.4% SL vs. 15.1–18.4), and more slender head (depth 13.0–16.4% SL vs. 17.0–20.2); and from *G. lampris* by its shorter pectoral-fin spine (12.7–17.8% SL vs. 19.6–24.7) and smaller eye diameter (7–11% HL vs. 13–17).

DISCUSSION

The single-gene analysis in this study was designed primarily to identify clades representing species of *Glyptothorax* in the Mae Klong River basin and not to rigorously test relationships among species. Nevertheless, with such a high number of available names described from the region to consider, as many taxa as could be sequenced or reliably sourced from GenBank were included in the tree, and certain clades representing species other than those in the Mae Klong and some above the species level are worth noting for the strong support achieved by Bayesian analysis of the COI locus. The phylogeny also contained taxonomic implications for several species of *Glyptothorax*, within and outside the Mae Klong basin.

Three species groups are represented as deep-rooted clades, two with high posterior probabilities (Fig. 1). The barred species clade (containing, e.g., *G. platypogonides*) and the uniformly dark-colored species clade (containing, e.g., *G. schmidtii*) had strong support in the BI analysis. Species possessing a complex thoracic adhesive apparatus (including *G. burmanicus* and *G. rugimentum*) were resolved outside either clade with strong support, but monophyly of this group was indicated with only moderate posterior probabilities. The ML analysis resolved the same general topology but with lower support values for all clades than in the Bayesian tree. The barred clade received moderately high bootstrap support, but the dark-colored clade and the clade containing species with a complex thoracic adhesive apparatus were recovered only in a slim majority of runs. The barred clade is not known to occur in or west of the Salween River, with the Mae Klong River being the westernmost extent of its range in mainland Southeast Asia. Species with a complex thoracic adhesive apparatus occur only in or west of the Salween River. The uniformly dark clade is more widespread, occurring from northern Sumatra north to China and west at least to India.

Glyptothorax platypogonides was recorded from the Ping River tributary of the Chao Phraya basin by Smith (1945) but was considered by more recent studies to range only as far north—from its type locality in Sumatra—as peninsular Thailand (Ng and Kottelat, 2016; Panitvong, 2020) or not to occur in Thailand (Vidthayanon, 2017). In the molecular analyses (Fig. 1), *G. platypogonides* was found to occur in the Mae Klong River basin in western Thailand and in the Chao Phraya River basin in central Thailand. Morphological comparison of specimens from Sumatra, the Malay peninsula, and mainland Thailand east to the Chao Phraya River found no appreciable phenotypic differences among populations (Fig. 2). The Chao Phraya River was indicated to be the easternmost distributional limit of the species in the molecular phylogeny (Fig. 1).

An apparently unnamed species in the Mekong River, first reported as *G. cf. lampris* by Jiang et al. (2011) and herein referred to as *G. aff. platypogonides*, is sister to and most closely resembles *G. platypogonides*. However, *G. platypogonides* and *G. aff. platypogonides* are much less closely related, at 6.38% dissimilarity of the COI gene (Table 3), than are the

Sumatran, peninsular, and mainland populations of *G. platypogonides* (Fig. 1). The Mekong River is home to several species lacking genetic data, and a more thorough morphological and genetic comparison of the putative new species to congeners in the basin is ongoing by the authors.

Glyptothorax lampris, recovered as sister to the clade containing *G. platypogonides* and *G. aff. platypogonides*, is reported for the first time from the Tapi River in peninsular Thailand. *Glyptothorax callopterus*, described from near Trang in peninsular Thailand, was found to be genetically distinct from *G. fuscus*, described from a Gulf of Thailand drainage in southeastern Thailand (Fowler, 1934), and is resurrected from synonymy.

Although external morphological differences separating the uniformly dark-colored species of the *G. trilineatus* clade remain unelucidated, *G. laosensis*—dubious since its original description as a possible synonym of *G. trilineatus* (Fowler, 1934; Smith, 1945)—is herein supported as valid and distinct from *G. trilineatus* based on a non-sister relationship between the two species as well as a 4.22% between-group p-distance (Table 3). *Glyptothorax trilineatus* does not occur in or east of the Salween River and is restricted to the Sittang and Irrawaddy Rivers of Myanmar. *Glyptothorax schmidtii* was recovered as sister to *G. laosensis*, with populations of *G. schmidtii* from the Mekong River in Thailand (OK077081, OK077082) and China (HQ593565) more closely related to one another (with 0.76% intraspecific p-distance, Table 3) than to populations of *G. laosensis* from the Thai and Chinese Mekong (with between-group p-distance of 3.13%), validating recognition of the two as separate species. *Glyptothorax laosensis* is found only in the Mekong River basin.

A uniformly dark-colored species present only in the upper and lower Salween River basin was found to be sister to the clade containing *G. schmidtii* and *G. laosensis*. Labeled *G. aff. trilineatus* on the phylogeny, the apparently undescribed Salween species was previously reported as *G. trilineatus* (Ng and Kottelat, 2008: fig. 5d; Jiang et al., 2012) but is shown to be genetically distinct from *G. trilineatus* topotype sequences from the Sittang River.

Glyptothorax longinema was recovered as sister to *G. granosus* in the Salween River, as reported by Jiang et al. (2012). Sequence data were generated for *G. dorsalis* from the Salween River and included for the first time in a phylogeny alongside the ten other Salween congeners, adding molecular support to the high number of species of *Glyptothorax* reported from that drainage (Jiang et al., 2012).

A tendency has been observed among species of *Glyptothorax* to occupy extremely restricted geographic distributions (Jiang et al., 2012; Ng and Kottelat 2017). However, one of the key findings of the present study was the expansion in the latitudinal range over which all species in the Mae Klong were known to occur, and increased sampling may show other species to be more widespread than assumed. *Glyptothorax platypogonides* and *G. schmidtii* were found to be much more wide-ranging than the already broad distributions reported by Ng and Kottelat (2016), with the inclusion of the Mae Klong–Chao Phraya and Mekong populations, respectively. *Glyptothorax longinema* was found to bridge an apparent ichthyofaunal divide between the upper (Chinese) and lower Salween (Abell et al., 2008) and to occur in the Mae Klong. The southern distributional limits of *G. buechanani* and *G. lampris* were extended to the Mae Klong and Tapi Rivers, respectively.

Despite its relatively small size, and although none of the representatives is endemic to its waters, the Mae Klong is

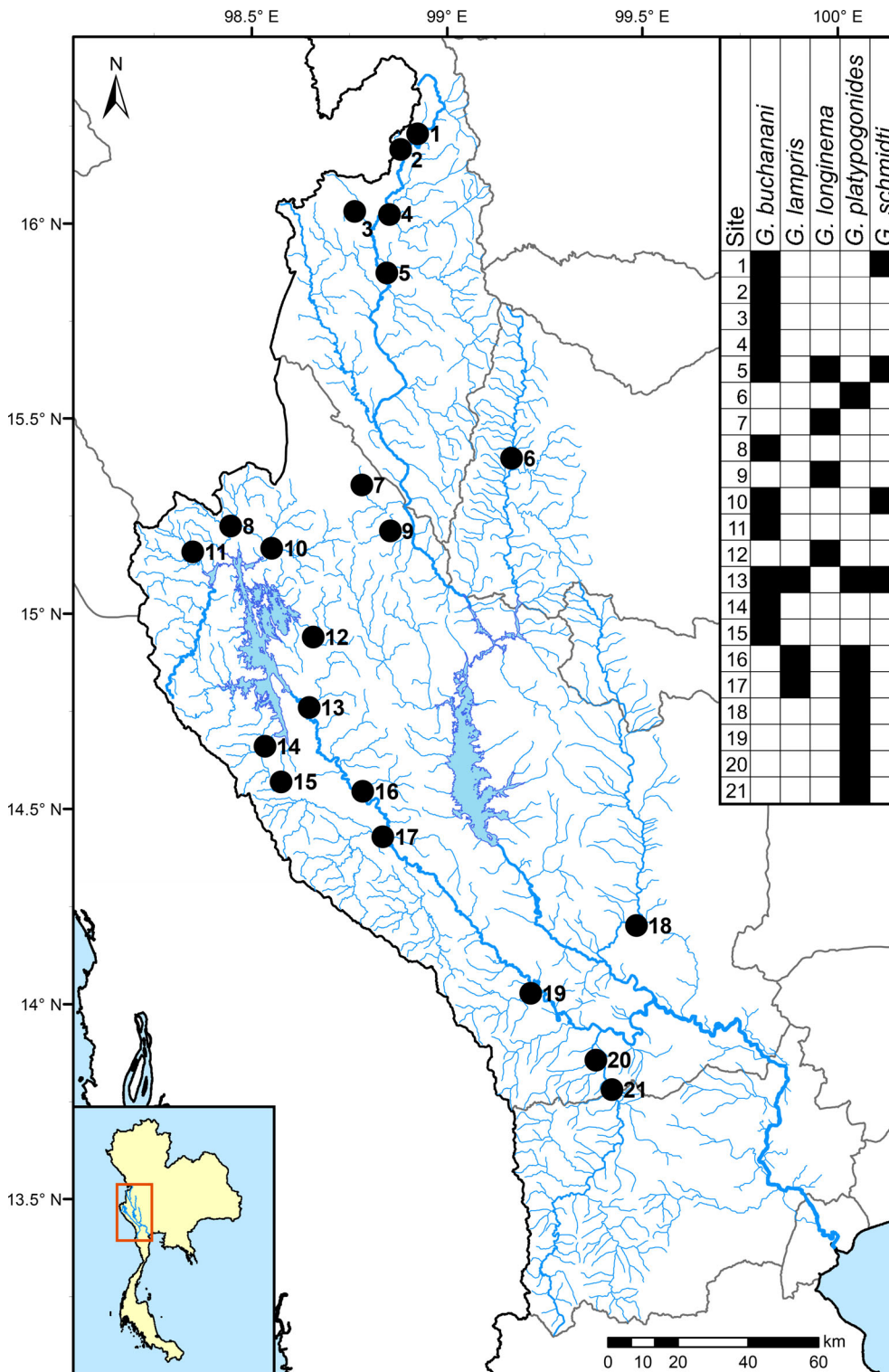


Fig. 14. Collection localities of species of *Glyptothorax* in the Mae Klong River basin.

home to a unique composition of species of *Glyptothorax*. With the adjacent Salween River, which claims at least 11 species between headwaters and delta, it shares only *G. longinema*. The Chao Phraya is home to three or four of the five Mae Klong species—all except *G. longinema* and possibly *G. lampris*—with populations of *G. buchanani*, *G. platypogonides*, and *G. schmidt* that are genetically inseparable, suggesting a close relationship between the basins. With the rivers of the Malay Peninsula the Mae Klong shares *G. lampris*, *G. platypogonides*, and *G. schmidt*.

All collections of *Glyptothorax* examined from the Mae Klong River basin were taken from the Khwae Noi or Khwae Yai, the principal tributaries of the basin. The only obvious distributional pattern to emerge between the two was the collection of *G. lampris* exclusively from localities along a relatively short segment of the Khwae Noi and not at all from the Khwae Yai (Fig. 14). The remaining four species in the Mae Klong River basin were collected in both tributaries.

Elevational gradient appeared to exert greater influence, with *G. buchanani*, *G. longinema*, and *G. schmidt* more



Fig. 15. Habitats of *Glyptothorax* in the Mae Klong River basin. (A) Pracham Mai River, 14.659°N, 98.534°E, 6 January 2017. (B) Mae Lamung Creek, 15.873°N, 98.846°E, 10 January 2018. (C) Confluence of Umphang Creek and Khwae Yai River, 16.022°N, 98.852°E, 10 January 2018. (D) U Long Creek, 14.759°N, 98.647°E, 23 January 2018. Photos by Zachary Randall, Florida Museum of Natural History.

widespread in upper elevation streams, with mean elevations of 322 (11 sites), 518 (4), and 320 (4) meters, respectively, and *G. lampris* and *G. platypogonides* captured more often in low-lying areas of the drainage, with mean elevations of 109 (3) and 95 (8) meters, respectively. As indicated in the principal component analysis (Fig. 2), *G. lampris* and *G. platypogonides*, those species living in low-lying areas, tend to have proportionally larger eyes, a shorter dorsal-to-adipose distance, and longer dorsal-fin spines than species living in more upland, typically faster-flowing, clear streams. At all localities, including the flatter and muddier sites in the southern part of the drainage, species of *Glyptothorax* were found to inhabit rocky riffles (Fig. 15).

KEY TO SPECIES OF *GLYPTOTHORAX* IN THAILAND

Morphological distinctions of the three species-pairs separated by river basin (*G. fuscus*–*G. callopterus*, *G. platypogonides*–*G. aff. platypogonides*, *G. laosensis*–*G. aff. trilineatus*) were not apparent in this study. Further study to elucidate phenotypic differences among these species is ongoing by the authors.

- | | | | |
|-----|--|----------------------------|----|
| 1a. | Thoracic adhesive apparatus extending onto gular region; Salween River | <i>G. rugimentum</i> | 2 |
| 1b. | Thoracic adhesive apparatus not extending onto gular region | | |
| 2a. | Thoracic adhesive apparatus with ovoid central pit; Salween River | <i>G. burmanicus</i> | |
| 2b. | Thoracic adhesive apparatus without ovoid central pit | | 3 |
| 3a. | Nuchal plate elements conspicuously pale, starkly contrasted against dark predorsal region | | 4 |
| 3b. | Nuchal plate elements inconspicuous, not in contrast to predorsal region | | 6 |
| 4a. | Nuchal plate elements pale anterior to dorsal origin; body without obvious mottling | | 5 |
| 4b. | Nuchal plate elements pale only on sides, inconspicuous anterior to dorsal origin; body with obvious mottling; Salween River | <i>G. ngapang</i> | |
| 5a. | Caudal peduncle slender, depth 6.8% SL or less; head short, 24.2% SL or less; Salween River | <i>G. dorsalis</i> | |
| 5b. | Caudal peduncle deep, 9.6% SL or greater; head long, 26.6% SL or greater; Mae Klong and Chao Phraya Rivers | <i>G. buchanani</i> | |
| 6a. | Skin rough, densely tuberculated; body pale-brown or with broad, irregular bars | | 7 |
| 6b. | Skin smooth, without prominent tubercles; body uniformly dark-brown to dark-gray, without bars | | 11 |
| 7a. | Three dark bars on body, one each below dorsal and adipose fins and one on caudal peduncle, with well- | | |

- defined, jagged margins; **Mae Klong**, Chao Phraya, Mekong, and peninsular rivers ***G. lampris***
- 7b. Bars on body with nebulous margins or absent 8
- 8a. Body slender, gently inclined dorsally from snout to dorsal origin; body often with irregular bars; dorsal-fin margin concave; caudal fin with one or two hyaline, chevron-shaped bands, sometimes absent 9
- 8b. Body deep, steeply inclined from snout to dorsal origin; body without bars, often with obvious mottling; dorsal-fin margin straight; caudal fin with longitudinal hyaline blotch between lobes 10
- 9a. **Mae Klong**, Chao Phraya, and peninsular rivers ***G. platypogonides***
- 9b. Mekong River *G. aff. platypogonides*
- 10a. Eastern Gulf of Thailand drainages in Chanthaburi and Trat provinces *G. fuscus*
- 10b. Peninsular rivers *G. callopterus*
- 11a. Nasal barbel long, reaching to eye; mid-dorsal and -lateral stripes thin, brown-beige, midlateral originating above gill opening; **Mae Klong** and Salween Rivers ***G. longinema***
- 11b. Nasal barbel not reaching eye; mid-dorsal and -lateral stripes, when present, thick, gold, mid-lateral originating at eye 12
- 12a. **Mae Klong**, Chao Phraya, eastern Gulf of Thailand and peninsular rivers ***G. schmidtii***
- 12b. Mekong and Salween Rivers 13
- 13a. Mekong River *G. laosensis*
- 13b. Salween River *G. aff. trilineatus*

COMPARATIVE MATERIAL EXAMINED

Glyptothorax burmanicus: Thailand: Salween drainage: Mae Hong Son: UF 183896, 3.

Glyptothorax callopterus: Malaysia: Golok drainage: Kelantan: UF 236160, 33. Thailand: Phang Nga River: Phang Nga: UF 183901, 4; UF 183902, 1; UF 183904, 1. Tapi drainage: Nakhon Si Thammarat: UF 183324, 5; UF 183899, 5; UF 183906, 7; UF 236110, 1. Surat Thani: UF 191831, 3. Tha Di River: Nakhon Si Thammarat: UF 183905, 5.

Glyptothorax dorsalis: Thailand: Salween drainage: Tak: UF 192232, 4; UF 192332, 3; data from Rameshori and Vishwanath (2014).

Glyptothorax fuscus: Thailand: Chanthaburi drainage: Chanthaburi: UF 235987, 15. Trat drainage: Chanthaburi: UF 169837, 1; UF 169838, 8; UF 188815, 4. Trat: UF 235947, 8.

Glyptothorax laosensis: Cambodia: Mekong drainage: Stung Treng: UF 190469, 1. Thailand: Mekong drainage: Ubon Ratchathani: UF 172618, 1; UF 185174, 2; UF 185202, 1.

Glyptothorax ngapang: Thailand: Salween drainage: Mae Hong Son: UF 183895, 14; UF 183900, 4; UF 190160, 2. Tak: UF 192338, 28; UF 192357, 18; UF 192415, 2.

Glyptothorax aff. platypogonides: Cambodia: Mekong drainage: Stung Treng: UF 190437, 5; UF 190459, 1. Laos: Mekong drainage: Champasak: UF 185482, 1. Thailand: Mekong drainage: Chiang Mai: UF 237477, 2. Ubon Ratchathani: UF 169839, 1; UF 184385, 1; UF 185175, 16; UF 185181, 9; UF 185228, 1.

Glyptothorax plectilis: Data from Ng and Kottelat (2016).

Glyptothorax rugimentum: Thailand: Salween drainage: Mae Hong Son: UF 183897, 3; UF 188293, 1; UF 188369, 1; UF 190158, 2. Tak: UF 192225, 1; UF 192330, 1.

Glyptothorax aff. trilineatus: Thailand: Phang Nga drainage: Phang Nga: UF 183898, 1. Salween drainage: Mae Hong Son: UF 188260, 1. Tak: UF 192233, 1.

DATA ACCESSIBILITY

Supplemental material, including sequence data, measurements and counts of material examined, tree file, and the R script used to generate the sheared principal component analysis, is available at <https://www.ichthyologyandherpetology.org/i2022045>. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

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