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Structure of the andropodium of the viviparous halfbeak genus *Nomorhamphus* (Atherinomorpha: Beloniformes: Zenarchopteridae), endemic to Sulawesi, Indonesia

Janina Kraemer[1*], Philipp Thieme[2], Renny Kurnia Hadiaty[**] & Fabian Herder[1]

Abstract. In halfbeaks (Zenarchopteridae), viviparity is known in three of the five genera, including *Nomorhamphus.* During the extremely short copulation, the transfer of spermatozeugmata from the male genital papilla to the female urogenital opening is apparently facilitated by the andropodium, an organ composed of the strongly modified male anterior anal-fin rays. Substructure of the andropodium varies among species, and traits of the modified anal-fin rays have been used as taxonomic characters for species delimitation. The present study examines the microanatomy of the andropodium across 11 of the 12 *Nomorhamphus* species, which are endemic to Sulawesi. Methods applied include contrast-enhanced µCT-imaging and clearing and staining approaches. Similarity in andropodial fin ray traits correlates with general morphology and spatial proximity. Species occurring in sympatry possess similar andropodia; the copulatory organ of *Nomorhamphus rex* is most distinct. In general, andropodial traits allow clear discrimination in most of the species examined, but require careful examination. The supposed incomplete calcification of the modified rays and their resulting flexibility provide arguments against the hypothesis of the andropodium as a true intromittent organ. The structure might rather help to orient the genital papilla in direction of the female genital opening during mating.

Key words. *Nomorhamphus,* andropodium, Sulawesi, freshwater halfbeaks, taxonomy, viviparity

INTRODUCTION

Internal fertilisation is a precondition for viviparity, which is characterised by the retention of developing eggs and embryos within the female reproductive tract (Wourms, 1981; Wourms & Lombardi, 1992), and occurs in at least three genera of the halfbeak family Zenarchopteridae (Schindler & Hamlett, 1993; Meisner, 2001; Lovejoy et al., 2004; Aschliman et al., 2005; Reznick et al., 2007). Parts of the anal fin of male Zenarchopteridae are modified to form an organ, the so-called 'andropodium' (Brembach, 1976; Fig. 1), which plays an uncertain role during copulation. The closely related freshwater SE-Asian halfbeak genera *Nomorhamphus* and *Dermogenys* share a similar configuration of the andropodium, with the first five to seven anal-fin rays shortened and thickened (Brembach, 1976; Meisner, 2001). The anal fins of *Hemirhamphodon* and *Zenarchopterus* are much less modified, and little is known about the reproductive morphology of the monotypic genus *Tondanichthys* (Anderson & Collette, 1991; Collette, 1995; Meisner, 2001; Tan & Lim, 2013). Though a number of studies have addressed aspects of reproduction in *Nomorhamphus* and *Dermogenys* (Mohr, 1936; Brembach, 1976; Meisner & Burns, 1997a, 1997b; Meisner, 2001; Greven, 2006, 2010), some fundamental questions remained unanswered, including the mechanism of sperm transfer during copulation.

Downing & Burns (1995) studied testis morphology and spermatozeugma formation, and concluded that during copulation sperm bundles are somehow transferred to the female genital pore by the help of the modified anal fin in *Dermogenys* and *Nomorhamphus*. The mating process lasts for several seconds in *Hemirhamphodon* and *Zenarchopterus,* during which the male achieves firm contact to the anal region of the female by clasping the female with its dorsal and anal fin. In *Nomorhamphus* and *Dermogenys*, mating is more rapid and lasts for ca. 40 ms (Kottelat & Lim, 1999; Greven, 2010). In *N. liemi* and *D. pusilla,* a putative copulation is characterised by an extremely quick axial rotation of the male and a forceful push against the female´s anal region (Magyar & Greven, 2007; Greven, 2010).

Brembach (1976) observed that anal-fin rays two to four can be splayed out laterally at an angle of 30°–40°, and hypothesised that they form a groove to direct the sperm bundles to the terminal structure of the second anal-fin ray, which 'spoons' the spermatozeugmata into the female genital opening. To achieve a position permitting the contact between

[1]Zoologisches Forschungsmuseum Alexander Koenig, Sektion Ichthyologie, Adenauerallee 160, D-53113 Bonn, Germany; Email: kraemer_janina@gmx.net (*corresponding author)

[2]Deutsches Meeresmuseum Stralsund, Katharinenberg 14-20, D-18439 Stralsund, Germany; Email: philipp.thieme@meeresmuseum.de

[**]Deceased.

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male and female, the andropodium would have to perform a 180°-rotation, as known for the poeciliid gonopodium (Meisner & Burns, 1997a). However, the effective mobility of both genital papilla and anal-fin rays is highly restricted due to the lack of musculature (Greven, 2010). Additionally, the female genital pore is small and a successful conjunction between male and female genital opening within 40 ms appears unlikely (Greven, 2010). Meisner & Burns (1997a) assumed that the andropodium of *Nomorhamphus* and *Dermogenys* may primarily serve to orient the genital palp of the male in direction of the female genital pore, similar to the andropodium of goodeids. The cryptoplica, a fleshy sheath forming a duct comprising the modified rays, may prevent the loss of sperm bundles.

Nomorhamphus species inhabit hill-stream habitats and freshwater lakes of Indonesia and the Philippines (Brembach, 1991; Kottelat & Whitten, 1996; Meisner, 2001; Collette, 2004; Kottelat, 2013; Miesen et al., 2015). With 12 endemic species, Sulawesi is named the hotspot of *Nomorhamphus* diversity; seven species occur on islands of the Philippines (Meisner, 2001; Huylebrouck et al., 2012, 2014). The structure of the andropodium varies between species and was used by several authors to define species limits within the genus and its sister group *Dermogenys* (Brembach, 1976, 1991; Meisner & Louie, 2000; Meisner, 2001; Huylebrouck et al., 2012, 2014). Detailed descriptions of the microanatomy of the andropodium were provided by Mohr (1936), Brembach (1976), Meisner (2001) and Huylebrouck et al. (2012). Brembach (1976) introduced the term andropodium, referring to the modified anal fin of the three viviparous genera *Hemirhamphodon*, *Dermogenys*, and *Nomorhamphus*, which was afterwards adopted by all other authors (e.g., Meisner, 2001; Greven, 2010; Huylebrouck et al., 2012, 2014).

The use of the andropodial microanatomy for purposes of taxonomy has remained rather restricted (Brembach, 1991; Meisner, 2001; Huylebrouck et al., 2012, 2014). For example, descriptions and drawings by Brembach (1976, 1991) do not provide enough details for species delimitations. Nevertheless, he recognised differences of the spiculus, a spine-shaped terminal structure of the second anal-fin ray (Fig. 1), in *Dermogenys* and *Nomorhamphus* but rated the taxonomic potential of this structure as low. Meisner (2001) noticed that species of *Nomorhamphus* can be divided into subgroups based on characteristics of the andropodium, particularly shape and segmentation of the spiculus. However, when comparing the drawings and descriptions she presented for different species, it becomes obvious that most of the information given is highly repetitive, and that the spiculus remains the only distinguishing feature. Since her study, three new species were described by Huylebrouck et al. (2012, 2014), who utilised "sub-segments" (minute subdivisions of segments) of the second, third and fourth anal-fin rays that are only visible in cleared and stained specimens as diagnostic traits. The present study compares the ultrastructure of the andropodium in 11 of the 12 species of *Nomorhamphus* from Sulawesi, and evaluates its taxonomic potential.

MATERIAL AND METHODS

Specimens used in this study are housed in the following museum collections: MZB, Museum Zoologicum Bogoriense, Bogor, Indonesia; WFB, Museum of Wildlife and Fish Biology, University of California, Davis, USA; ZFMK, Zoologisches Forschungsmuseum Alexander Koenig, Leibniz Institute of Animal Biodiversity, Bonn, Germany; ZMH, Zoologisches Museum Hamburg, Hamburg, Germany; ZSM, Zoologische Staatssammlung München, Munich, Germany. Measurements of the standard length (SL) were taken from the tip of the upper jaw to the base of the caudal fin, recorded to the nearest 0.1 mm with a digital calliper. We follow classification resulting from the phylogenetic revision of Meisner (2001) and the species descriptions of Huylebrouck et al. (2012, 2014). The species status of *N. hageni* is highly questionable, as the few fishes left over from the type series are in very poor condition and the type locality is not known with certainty (Weber & de Beaufort, 1922; Mohr, 1936; Brembach, 1991; Meisner, 2001). This taxon was excluded from the present study.

CT scanning and three-dimensional visualisation. In total, 22 male *Nomorhamphus*, belonging to 11 species (2 specimens per species) were computed tomography (CT) scanned. Prior to scanning, specimens were transferred to plastic tubes containing 80% EtOH solution. The fishes were fixed firmly inside the tube using small pieces of plastic to avoid movements during the scanning process. All specimens were scanned with a 100 kV SkyScan 1272 desk-top X-ray microtomograph (Bruker microCT, Kontich, Belgium). The scanning parameters were 50–60 kV source voltage, 166–200 µA source current, 173–1,039 ms exposure time, camera binning = 2 × 2, frames acquired over 180°, 5–7 µm voxel resolution, filter = Al 0.25 mm, no oversize-scanning, 0.1° angular step size, frame averaging = 6–7, random movement = 15. Digital section reconstruction of the scans to 16 bit tagged image file format (TIFF) image stacks was done without compression by the software NRecon 1.7.1 provided by the Skyscan 1272 system (misalignment compensation = 1.0–5.5, ring artefacts reduction = 4, beam-hardening correction = 8%). Reduction of data size was achieved with DataViewer Version 1.5.4 (Bruker microCT, Kontich, Belgium) by selecting a VOI (Volume of Interest). DrishtiImport Version 2.6.4 was used to convert the data. Volume rendering of the dataset for three-dimensional exploration and visualisation was performed in Drishti Version 2.6.4 (Limaye, 2012).

Clearing and staining. Fourteen male *Nomorhamphus* representing all species except *N. weberi* were cleared and double stained with alcian blue for cartilage and alizarin red S for bone following the protocol based on Dingerkus & Uhler (1977) and Taylor & van Dyke (1985). Additional cleared and stained specimens available in the collections of ZFMK and ZMH were also examined.

Light microscopy. Specimens were investigated using an OLYMPUS SZX 12 and an OLYMPUS BX 51 microscope (Olympus Corporation, Tokyo, Japan), for comparison with the results achieved by CT scanning and clearing and staining

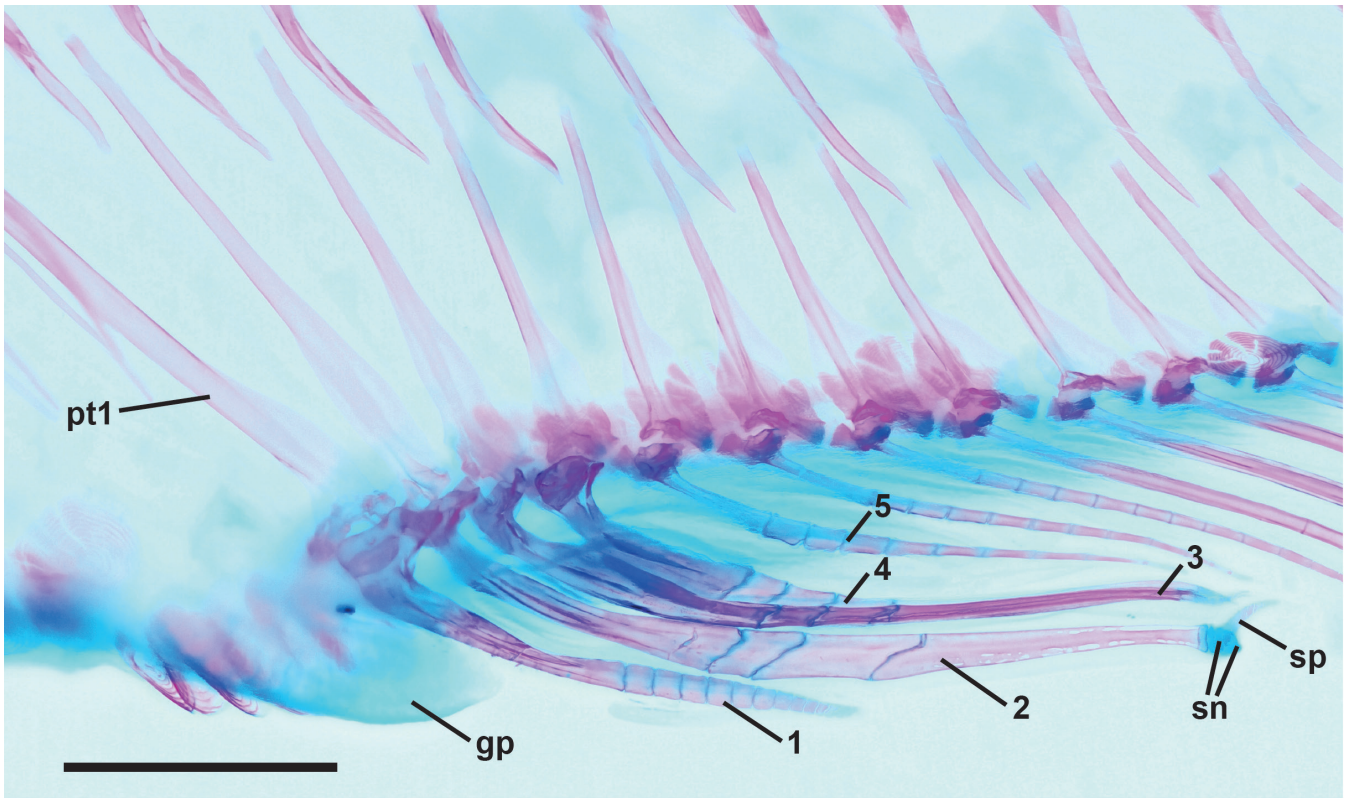

Fig. 1. Andropodium of *Nomorhamphus rex,* ZFMK 44945, 35.0 mm SL, cleared and double stained. Scale bar = 1 mm. Abbreviations: gp, genital papilla; pt1, first anal pterygiophore; sn, spinae = spines; sp, spiculus; 1–5, anal-fin rays one to five. The elongate genital papilla (gp) covers the anterior part of the first anal-fin ray (1). Anal-fin rays one to five are modified and considered as andropodium. The second anal-fin ray (2) is most strongly modified with a terminal structure, the tridens flexibilis, consisting of a central spiculus (sp) and two lateral spines (sn). The physa is a pouch-shaped structure located between the third (3) and fourth fin ray (4). In the freshly fixed specimen, the andropodium is covered by a fleshy sheath, the cryptoplica.

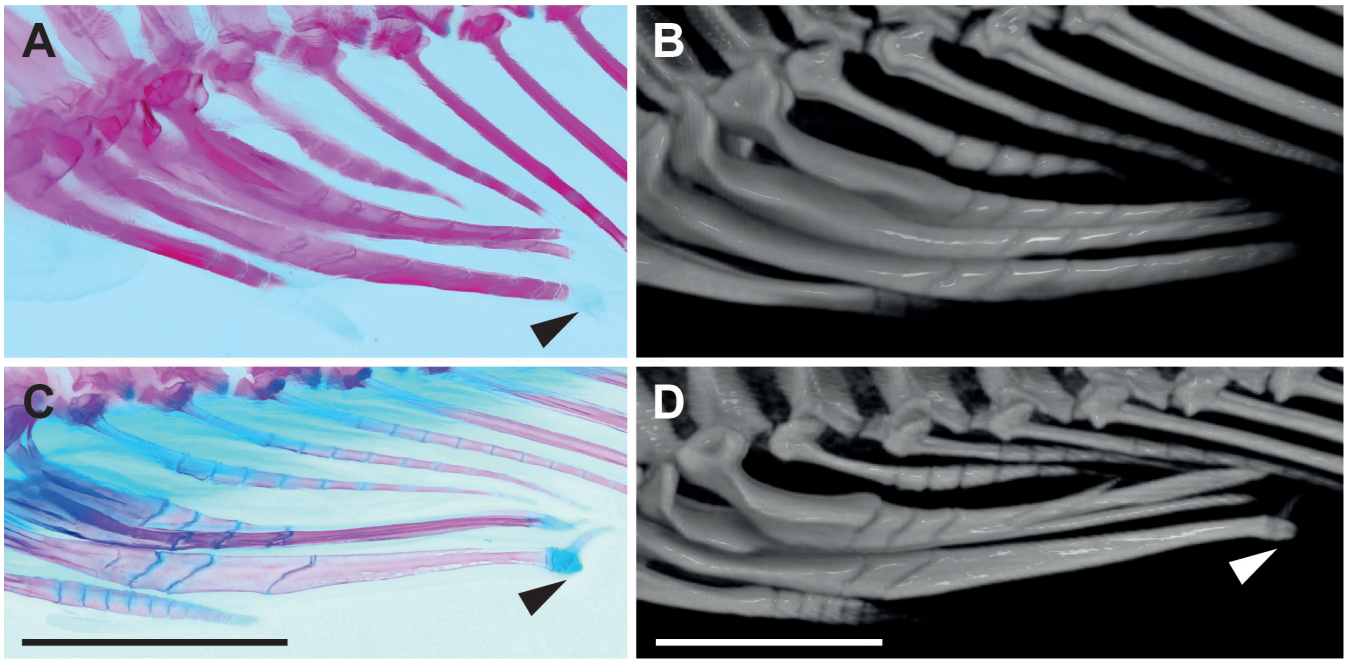

Fig. 2. A, B, Andropodium of *Nomorhamphus celebensis,* ZFMK 49216–49229, 39.4 mm SL. A, cleared and double stained; B, Rendered image. C, D, Andropodium of *N. rex*, (C) ZFMK 44945, 35.0 mm SL; (D) ZFMK 44944, 41.2 mm SL. C, cleared and double stained; D, rendered image. Scale bar = 1 mm. Arrowheads point to distal part of the second anal-fin ray, the tridens flexibilis.

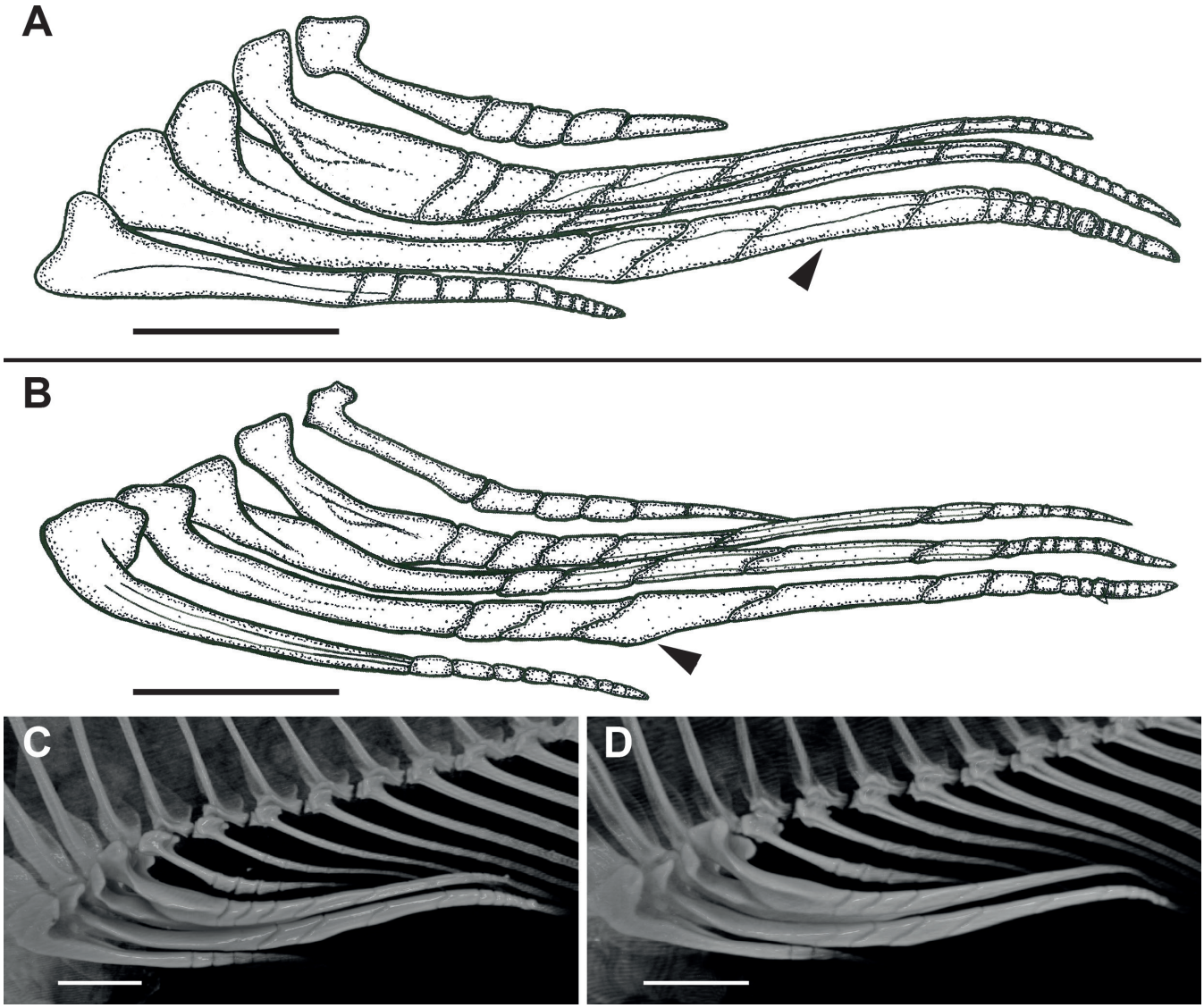

Fig. 3. A, B, diagrammatic representation of andropodium of (A) *Nomorhamphus brembachi,* ZMH 7616, 50.5 mm SL and (B) *N. liemi,* ZMH 7157, 36.6 mm SL. C, D, rendered image of andropodium of (C) *N. brembachi,* MZB 14450, 46.0 mm SL and (D) *N. liemi,* MZB 14473, 41.1 mm SL. Scale bar = 1 mm. Bone stippled. Arrowheads point (A) to sub-segments of second fin ray of *N. brembachi* and (B) to "geniculus" of *N. liemi*.

methods. A camera lucida was used to produce line drawings of the andropodia.

Terminology. Nomenclature of andropodial microanatomy follows Brembach (1976) and Huylebrouck et al. (2012, 2014).

RESULTS

The *Nomorhamphus* species from Sulawesi, except for *N. rex* (Fig. 1), are rather similar in their andropodial traits, but can be distinguished by the substructure of their second anal-fin ray (Figs. 2–6). The andropodium of each species resembles at least one other species. Thus, these 10 species were divided into four groups of morphologically similar andropodia: (1) *N. brembachi* & *N. liemi*; (2) *N. ebrardtii*, *N. lanceolatus*, & *N. sagittarius*; (3) *N. megarrhamphus* & *N. weberi*; (4) *N. celebensis*, *N. kolonodalensis*, & *N. towoetii*.

Descriptions of andropodia and anal-fin pigmentation

Nomorhamphus brembachi & N. liemi
(Fig. 3)

Pigmentation. *N. brembachi*: Posterior half of fin with black or brown pigment. *N. liemi*: Larger concentration of melanophores, anal fin completely black in many males. Both species: cryptoplica and base of fin rays hardly pigmented.

Andropodium. 1st anal pterygiophore thickened, not angled anteriorly. 2nd fin ray with 10–11 segments proximal to paired spinae; segments 2/3–10/11 with longitudinal groove in the middle separating these segments into dorsal and ventral part (*N. brembachi*), with or without three distinct longitudinal rows (*N. liemi*) without further sub-segments; segment 4/5 or both elongate; spiculus straight, clearly segmented at proximal end, broad tip, distal tip not in contact with tip of third fin ray; distal half of second fin ray curved dorsally

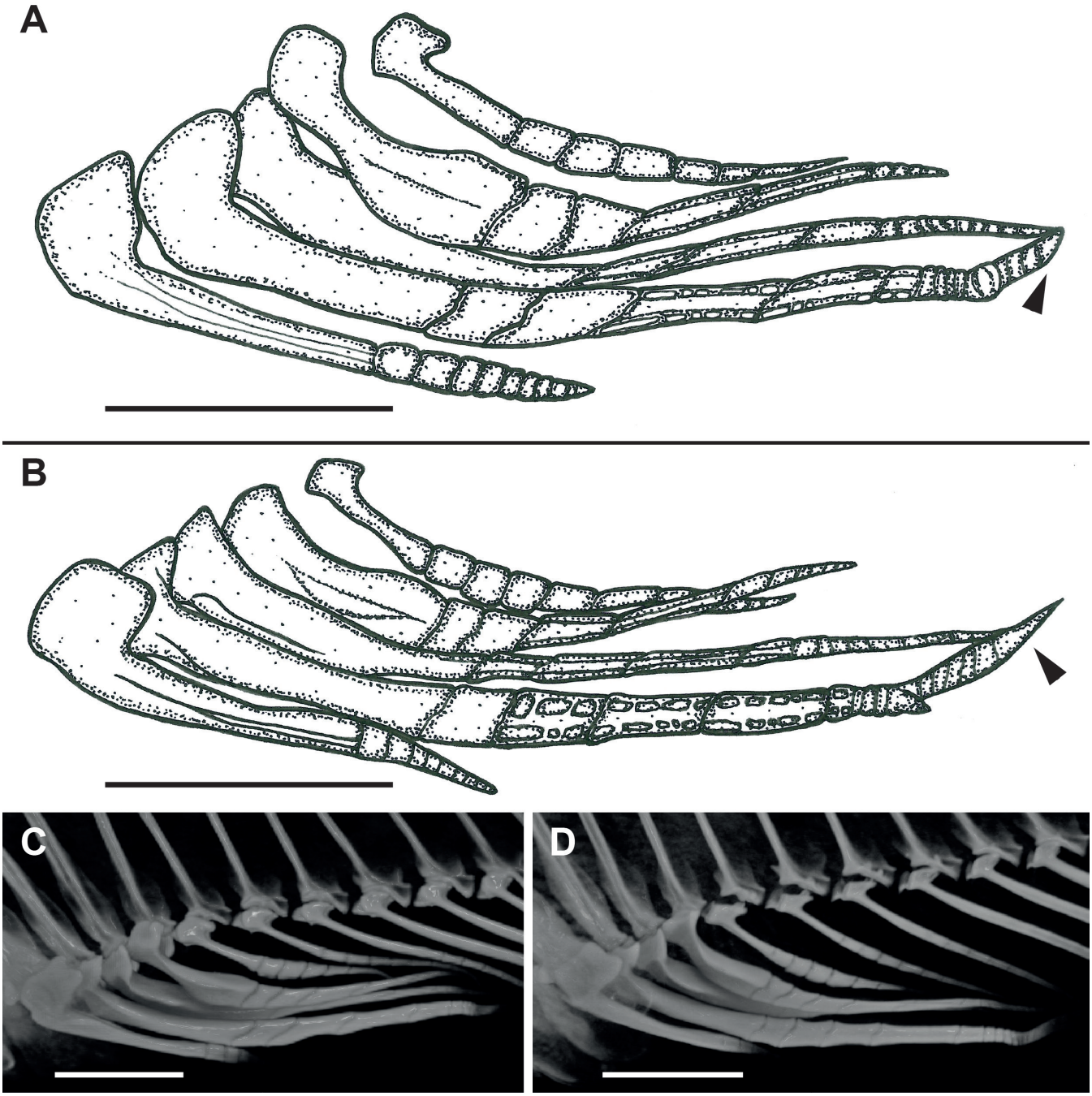

Fig. 4. A, B, Diagrammatic representation of andropodium of (A) *Nomorhamphus ebrardtii,* ZFMK 49156–49176, 40.0 mm SL and (B) *N. sagittarius,* MZB 20443, 35.2 mm SL. C, D, rendered image of andropodium of (C) *N. ebrardtii* and (D) *N. sagittarius,* WFB 3129, 39.3 mm SL. Scale bar = 1 mm. Bone stippled. Arrowheads point to spiculi of *N. ebrardtii* (A) and *N. sagittarius* (B), which contact the third anal-fin ray and differ in length.

with tip pointing ventrally. Some specimens of *N. liemi* with small geniculus at proximal half of segment 4. 3rd fin ray with segments 3–6 composed of three longitudinal rows, each row approximately 1/3 the height of the respective segment; segments 7 to tip short, tip straight. 4th fin ray with segments 4–5 exhibiting longitudinal groove in the middle separating these segments into dorsal and ventral part (*N. brembachi*) or composed of three longitudinal rows (*N. liemi*); segments 6–7/8 composed of three longitudinal rows, each row approximately 1/3 the height of the respective segment; following segments short. 5th fin ray with segments 2–4 thickened, shortened, approx. half the length of 4th fin ray.

Nomorhamphus ebrardtii*, *N. lanceolatus*, & *N. sagittarius
(Fig. 4)

Pigmentation. Lack of black pigment at posterior anal fin rays, cryptoplica and fin rays with few and small melanophores.

Andropodium. 1st anal pterygiophore thickened, not angled anteriorly. 2nd fin ray with 9–10 (7–10 in *N. sagittarius*) segments proximal to spinae; segments 3/4–6/7/8 with a dorsal and ventral row of differently sized sub-segments (squares, rectangles), each sub-segment approximately 1/3

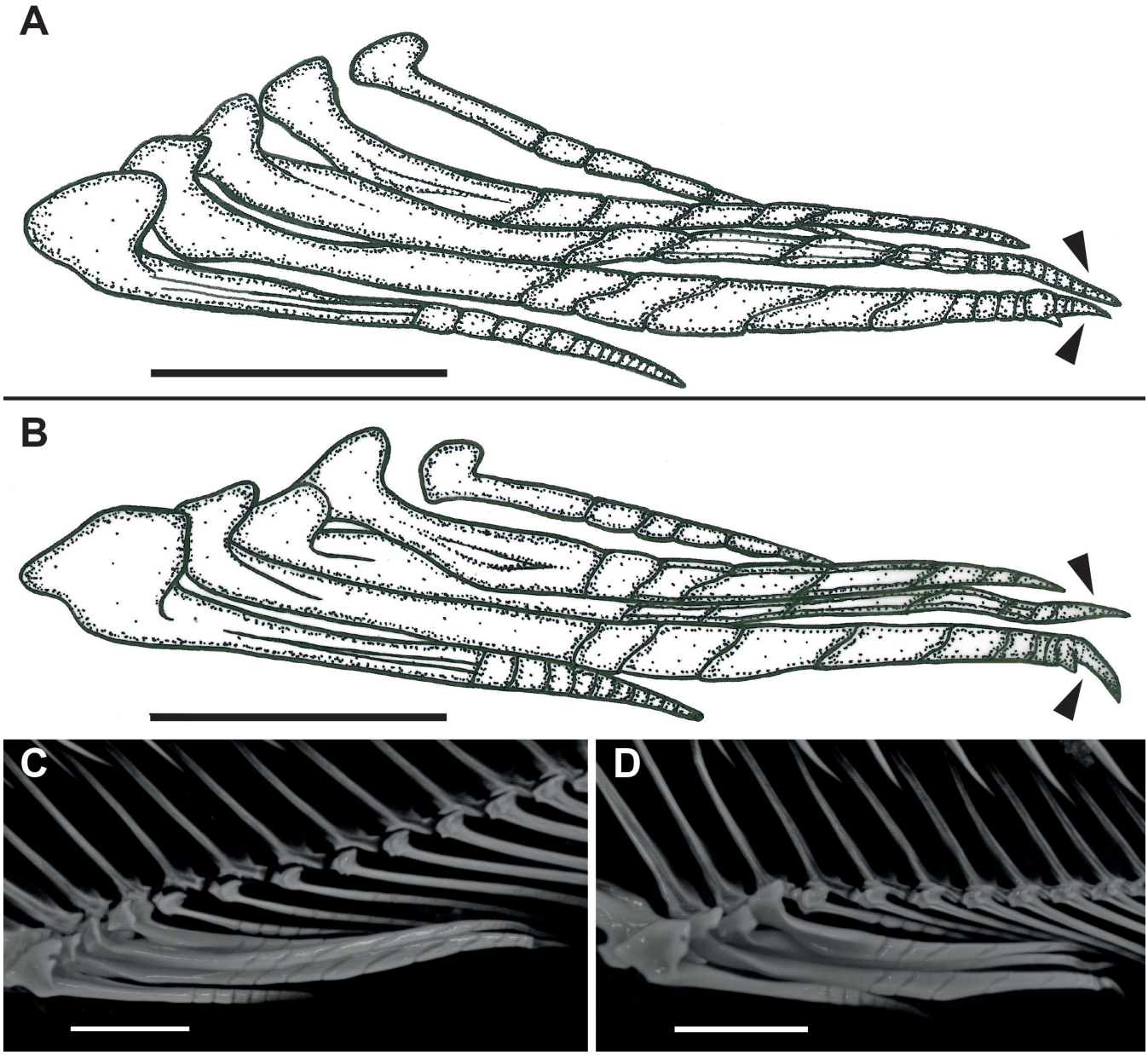

Fig. 5. A, B, diagrammatic representation of andropodium of (A) *Nomorhamphus megarrhamphus,* ZMH 7153, 38.3 mm SL and (B) *N. weberi,* ZMH 7970, 41.5 mm SL. C, D, rendered image of andropodium of (C) *N. megarrhamphus,* ZMH 7153, 43.4 mm SL and (D) *N. weberi.* Scale bar = 1 mm. Bone stippled. Arrowheads point to spiculi of *N. megarrhamphus* (A) and *N. weberi* (B) and tips of the third anal-fin ray.

the height of the respective segment; segments 4–5 elongate in large males; spiculus lanceolate, clearly segmented at proximal end, ventrally slightly curved, pointed dorsally at an angle of 45°, distal tips (middle segments in *N. lanceolatus* and *N. sagittarius*) of spiculus and 3rd fin ray in contact. 3rd fin ray slightly constricted longitudinally; segments 2–3 or 3–5 composed of three longitudinal rows, each row approx. 1/3 the height of the respective segment. 4th fin ray with distal half of segment 1 thickened; distal half of ray slightly constricted longitudinally; segments 4–5/6/7 elongate and composed of three longitudinal rows, each row approximately 1/3 the height of the respective segment. 5th fin ray not noticeably thickened (*N. ebrardtii)* or segments 2–5 thickened, (*N. lanceolatus, N. sagittarius*).

Nomorhamphus megarrhamphus* & *N. weberi
(Fig. 5)

Pigmentation. Lack of black pigment at posterior anal fin rays, few and small melanophores at cryptoplica and base of fin rays.

Andropodium. All males investigated are lacking a physa and the cryptoplica is weakly developed, covering only a small basal part of the andropodial fin rays. The anal-fin rays forming the andropodium appear less curved and modified compared to other species. 1st anal pterygiophore thickened, angled anteriorly. 2nd fin ray with 9–11 segments proximal to spinae; segments 3–5 broader than all other segments of the 2nd fin ray. *N. megarrhamphus*: spiculus clearly segmented at proximal end, short and thin, dorsal

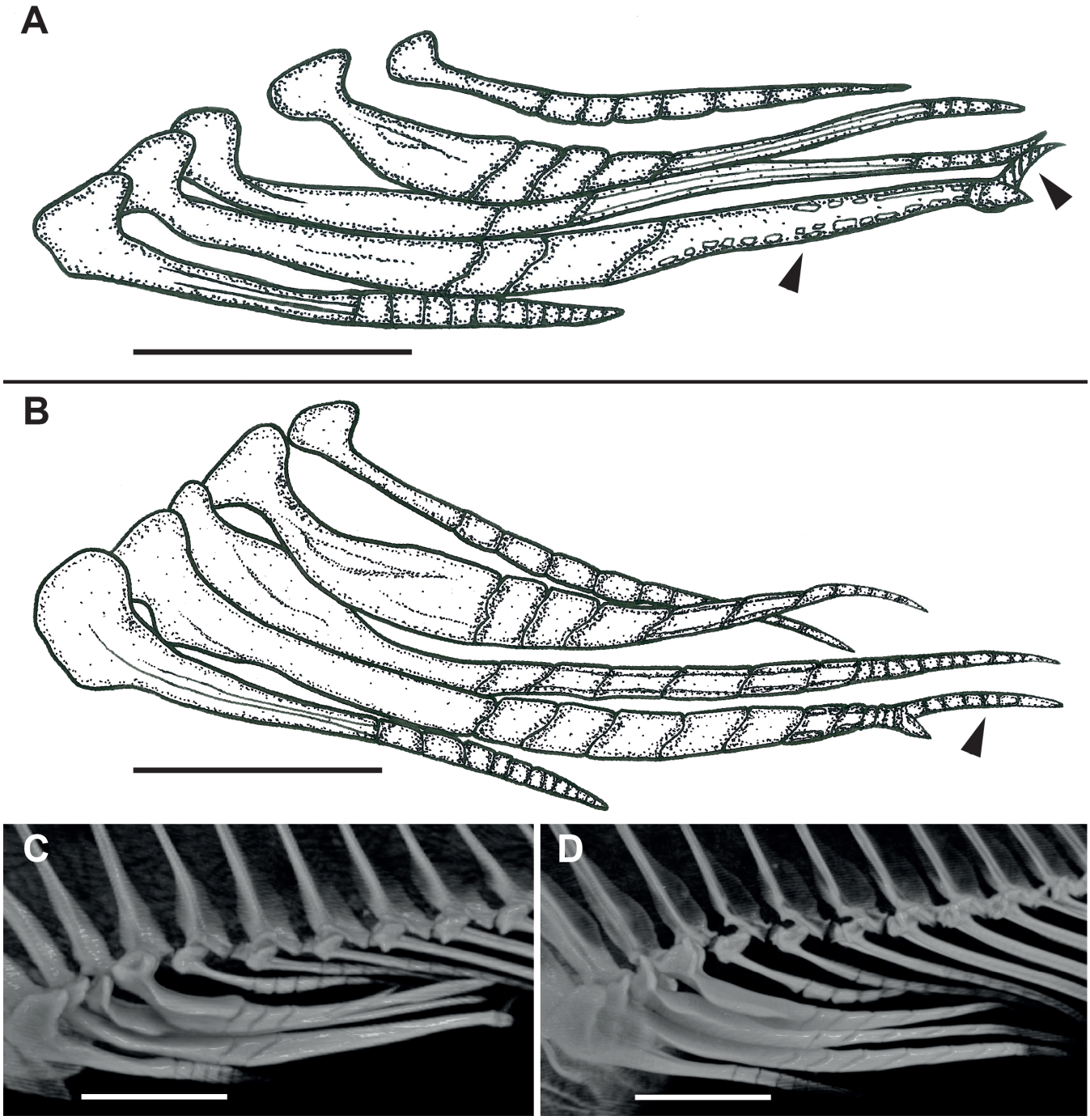

Fig. 6. A, B, Diagrammatic representation of andropodium of (A) *Nomorhamphus rex,* ZFMK 44945, 35.0 mm SL and (B) *N. kolonodalensis,* ZFMK 49103, 40.3 mm SL. C, D, Rendered image of andropodium of (C) *N. rex,* ZFMK 44944, 41.2 mm SL and (D) *N. kolonodalensis.* Scale bar = 1 mm. Bone stippled. Arrowheads point (A) to the elongate fourth segment of the second anal-fin ray and to the characteristic, sickle-shaped spiculus of *N. rex* and (B) to the thin, elongate spiculus of *N. kolonodalensis*.

portion slightly curved, in contact with distal segments of 3rd fin ray. *N. weberi*: sickle-shaped spiculus, not clearly segmented, pointed ventrally, not in contact with tip of 3rd fin ray. 3rd fin ray with segments 2/3–6/7 composed of three longitudinal rows, each row approximately 1/3 the height of the respective segment. 4th fin ray approximately as broad as 2nd fin ray. *N. weberi*: segments 3–5 composed of three longitudinal rows, each row approximately 1/3 the height of the respective segment. 5th fin ray thin, not noticeably thickened.

Nomorhamphus rex
(Fig. 6A, C)

Pigmentation of anal fin. Distal tips of anal-fin rays greyish or black in most males; range and intensity of pigmentation varies between individuals; cryptoplica and fin rays slightly pigmented, small melanophores.

Andropodium. 1st anal pterygiophore thickened, not angled anteriorly. 2nd fin ray with 3–4 segments proximal to spinae; segment 3 or 4 greatly elongate, approximately half the length of the entire ray, with an irregular dorsal and

ventral row of small sub-segments (squares and rectangles) of different sizes, each sub-segment approximately 1/3 the height of segment 3 or 4, number of sub-segments variable; spiculus sickle-shaped, clearly segmented, short, upright position and curved (degree of curvature varies between specimens), its proximal and middle segments in contact with the distal tip of the third anal-fin ray. 3rd fin ray with segment 3 greatly elongate, approximately half the length of the entire ray, constricted longitudinally, composed of three longitudinal rows, each row approximately 1/3 the height of the respective segment; segments 4 to tip short, tip nearly straight. 4th fin ray with segment 4 composed of three longitudinal rows, greatly elongate; following segments short. 5th fin ray thickened in larger males.

Nomorhamphus celebensis*, *N. kolonodalensis*, & *N. towoetii
(Fig. 6B, D)

Pigmentation. Cryptoplica and fin rays slightly or not pigmented. *N. celebensis*: anal fin completely dusky and without distinctly black tips, higher concentration of melanophores compared to *N. kolonodalensis*. *N. kolonodalensis*: distal tips of anal-fin rays distinctly black; in smaller males only dorsal tips, in larger males dorsal 2/3. *N. towoetii*: distal tips of anal-fin rays with diffuse grey or black pigmentation or anal-fin completely dusky.

Andropodium. 1st anal pterygiophore thickened, not angled anteriorly. 2nd fin ray with 9/10–11 segments proximal to spinae. *N. kolonodalensis*: segments 7–8 in some specimens with dorsal and ventral row of irregular sub-segments (≥ 1, squares, rectangles), each segment approximately 1/3 the height of segment 7 or 8; spiculus only segmented at proximal end (*N. celebensis*) or spiculus clearly segmented (*N. kolonodalensis*), dorsal portion slightly curved or straight, not thickened, elongate in large males, not in contact to tip of 3rd anal fin ray. 3rd fin ray with segments 3/4–5/6/7 composed of three longitudinal rows, each row approximately 1/3 the height of the respective segment; tip of ray 3 nearly straight, parallel to spiculus. 4th fin ray: *N. kolonodalensis*: distal half thin and dorsal portion curved; segments 5–6/7 composed of three longitudinal rows, each row approximately 1/3 the height of the respective segment. 5th fin ray with segments 2–4 slightly thickened in *N. celebensis*, not thickened in *N. kolonodalensis* and *N. towoetii.*

Differences between populations of *Nomorhamphus towoetii*. Balambano River (ZFMK 49297–49299) – 2nd fin ray: spiculus straight, clearly segmented, contacts distal tip of 3rd fin ray. 3rd fin ray with segments 3–6 composed of three longitudinal rows, each row approximately1/3 the height of the respective segment. 4th fin ray with segments 4–7 composed of three longitudinal rows, each row approximately1/3 the height of the respective segment.

Southeast of Lake Matano (ZFMK 48960–49000) – 2nd fin ray: segment 9 with dorsal and ventral row of irregular sub-segments (≥ 1, squares, rectangles), each segment approximately1/3 the height of segment 9, spiculus straight, clearly segmented, no contact to tip of 3rd fin ray. 3rd fin ray with segments 2–6/7 composed of three longitudinal rows, each row approximately1/3 the height of the respective segment. 4th fin ray with segments 5–7 composed of three longitudinal rows, each row approximately1/3 the height of the respective segment.

North of Lake Poso (ZFMK 49177–49215); North of Lake Matano (ZFMK 49119–49146) – 2nd fin ray with spiculus straight, no contact to tip of 3rd fin ray but tips close.

Microanatomy of the andropodium. The first segment of the first anal-fin ray has a characteristic shape. It comprises approximately half the length of the total fin ray, is slightly constricted longitudinally and a groove in the middle of the segment gives the appearance of a longitudinal fission (Fig. 1). The number of segments contained in the first fin ray is intraspecifically highly variable. Larger males tend to have more segments than smaller males. The second fin ray usually lacks a distinct geniculus as present in *Dermogenys* spp., but in some specimens of *N. liemi* a small, geniculus-like "knee" is present (Meisner, 2001: Fig. 3B). The second fin ray comprises segments of different length, the size of these segments varies from proximal to distal, with the smallest segment situated prior to the basal segment of the spinae. *Nomorhamphus rex* is considered to be an exception, as the third or fourth segment is greatly elongate, followed by a minute segment prior to the spines (Figs. 1, 6A). The andropodium of *N. rex* is unique and can be distinguished from all others due to its low number of segments prior to the spines and the pronounced, sickle-shaped spiculus (Fig. 6A, C).

Six out of 11 species considered (*N. ebrardtii*, *N. kolonodalensis*, *N. lanceolatus*, *N. rex*, *N. sagittarius*, some populations of *N. towoetii*) possess irregular dorsal and ventral rows of small sub-segments in the central part of the second fin ray. In all species investigated, two grooves in the segments of the third and/or fourth fin ray give the appearance of segments composed of three longitudinal rows. The presence or absence of sub-segments in the second fin ray and longitudinal rows in the third and fourth fin ray is characteristic for each species, although number of sub-segments and expansion are slightly varying between the individuals. In the first and fifth fin ray, neither such modifications are present. The distal segments of fin rays 1 to 5 are flexible in the vast majority of investigated specimens.

ARTIFICIAL KEY BASED ON ANDROPODIAL CHARACTERS

For distinguishing the *Nomorhamphus* species of Sulawesi, this identification key is mainly based on features of the second anal-fin ray with emphasis on the spiculus. Five of 11 species are not clearly definable by andropodial features alone; these species are: *N. celebensis*, *N. kolonodalensis*, *N. lanceolatus*, *N. sagittarius*, and *N. towoetii.*

1. Pterygiophore angled anteriorly, physa absent, cryptoplica poorly developed, lack of black pigment at posterior anal-fin rays.....2
– Pterygiophore not angled anteriorly, physa present, cryptoplica well developed in mature males.....3
2. Spiculus clearly segmented at proximal end, short, not thickened, only slightly curved, contacts tip of 3rd fin ray..... .....*Nomorhamphus megarrhamphus*
– Spiculus not clearly segmented, sickle-shaped, strongly curved, tip points ventrally, not in contact with tip of 3rd fin ray..... .....*N. weberi*
3. 2nd fin ray with 3 to 4 segments proximal to spines, 3rd or 4th segment approx. half the length of the entire ray .....*N. rex*
– 2nd fin ray with 7 to 11 segments proximal to spines.....4
4. Spiculus lanceolate, ventral portion slightly curved, points dorsally at an angle of 45°, its middle segment or distal tip contacts distal tip of 3rd fin ray.....5
– Spiculus not lanceolate, curved or straight 6
5. Spiculus elongate, middle segments contact distal tip of 3rd fin ray .....*N. lanceolatus*, *N. sagittarius*
– Spiculus not elongate, distal tip contacts distal tip of 3rd fin ray .....*N. ebrardtii*
6. 2nd fin ray: segments 2/3–10/11 with longitudinal groove or composed of three longitudinal rows without smaller sub-segments, segment 4/5 or both elongate, spiculus straight, clearly segmented at proximal end, broad tip, not in contact with tip of 3rd fin ray.....7
– 2nd fin ray: segments without further segmentation, spiculus slightly curved dorsally or straight, not thickened, elongate in large males, parallel to distal tip of 3rd fin ray..... .....*N. celebensis*, *N. kolonodalensis*, *N. towoetii*
7. 2nd fin ray: segments 2/3–10/11 with longitudinal groove separating segments into dorsal and ventral part..... .....*N. brembachi*
– 2nd fin ray: segments 2/3–10/11 with or without three indistinct longitudinal rows, proximal end of segment 4 with small geniculus in many males.....*N. liemi*

DISCUSSION

In *Nomorhamphus*, andropodial traits vary conspicuously with geographic proximity, and are consistent throughout morphologically similar groups of species that occur in sympatry (e.g., *N. brembachi* and *N. liemi* compared to *N. rex*). Species with similar andropodial traits tend to share a similar overall gestalt, and are often restricted to the same habitat (e.g., *N. megarrhamphus* and *N. weberi*). This pattern seems to be more common in *Nomorhamphus* than in *Dermogenys*, a genus with a much broader distribution throughout fresh and brackish waters of Southeast Asia (Meisner, 2001). *Dermogenys* species can be defined easily by the shape of their andropodium, as males of allopatric species show remarkable differences in the microanatomy of their anal fin (Meisner, 2001).

Meisner (2001) described the spiculus of *N. brembachi* and *N. liemi*, two morphologically similar species from the highland of Maros, as thick, short and laterally expanded. In this study, the spiculus was found to be segmented at its proximal end and lacking the contact to the tip of the third anal-fin ray. As mentioned by Meisner (2001), the dorsal portions of anal-fin rays two to four are curved in their distal half, which gives the andropodium a distinctly curved shape. Huylebrouck et al. (2014) described two species from Sulawesi Tenggara with a lanceolate spiculus, which show remarkable similarities to *N. ebrardtii,* whose spiculus was previously reported to be elongate, curved ventrally and in contact to the third anal-fin ray (Meisner, 2001). *Nomorhamphus lanceolatus* can be distinguished by its shorter lower jaw and the black fin pigmentation, which is absent in *N. sagittarius* and *N. ebrardtii* (Huylebrouck et al. 2014). *Nomorhamphus sagittarius* has a deeper body and an elongate lower jaw compared to *N. ebrardtii*.

Nomorhamphus megarrhamphus and *N. weberi*, both endemic to the freshwater lakes Towuti and Matano, are characterised by a slender, elongate body and an extremely elongate lower jaw (Meisner, 2001). The findings of Brembach (1991), who described their cryptoplica as weakly developed and the absence of a physa, a pouch-shaped structure located between the third and fourth anal-fin ray, were confirmed in the present study. Brembach (1991) assumed the physa to be involved in sperm-storage, but its absence in mature males questions this hypothesis, as it seems not to be necessary for successful mating (Brembach, 1976, 1991). Another peculiarity of the two lake-dwelling species is their first anal pterygiophore, which is angled anteriorly at a sharper angle compared to all other species. *Nomorhamphus weberi* differs from *N. megarrhamphus* in having a sickle-shaped and unsegmented spiculus.

Nomorhamphus celebensis, *N. kolonodalensis*, and *N. towoetii* possess a relatively unspecific andropodium and are difficult to identify by this structure alone. Common to both is the straight spiculus, which is not thickened but elongate in large males (Brembach, 1991; Meisner & Louie, 2000; Meisner, 2001). It is distinctly segmented in most specimens of *N. kolonodalensis* and *N. towoetii,* but differs in *N. celebensis* in that only the proximal end is segmented. The spiculus is more or less parallel to the tip of the third anal-fin ray. In *N. towoetii,* substantial differences between four populations were recorded, mainly concerning the composition of the third and fourth anal-fin ray. *Nomorhamphus towoetii* is widely distributed in the Malili Lakes region and the Lake Poso region (Meisner, 2001) with some populations completely isolated from each other, favouring a high variability in morphological traits. In contrast, variability within andropodial features was absent in species with a small distribution, such as *N. lanceolatus* and *N. brembachi*.

Taxonomic relevance of the modified anal-fin rays. Brembach (1991) clearly underestimated the taxonomic potential of the andropodium in *Nomorhamphus* when stating that it offers no utility for species delimitation. Nevertheless, careful observations of the anal fin on the basis of cleared and stained specimens were not adequate to clearly distinguish all of the 11 species investigated. Thus, further parameters such as fin pigmentation and jaw length should be incorporated. *Nomorhamphus rex* has an andropodium unique among all *Nomorhamphus* described so far (Huylebrouck et al., 2012). It mainly differs from the andropodium of other species in that the number of segments proximal to the spines is greatly reduced to three or four remaining segments versus

seven or more in other *Nomorhamphus*. Thus, the condition present in *N. rex* is considered as a derived state, potentially originating from the fusion of a higher number of segments.

Function of the andropodium. In most of the rendered images, the tips of the first and second anal-fin rays, including the spiculus, were not visible, although the resolution was high (Fig. 2B, D). Accordingly, the fin rays of all cleared and stained specimens were unstained at their tips or stained with alcian blue exclusively (Fig. 2A, C). In detail, the last few segments of the first fin ray, at least the distal tip of the spiculus and the tip of the third fin ray appeared to be not completely ossified or to possess very thin ossifications that might have been decalcified during the staining process. Similar results were obtained in the studies by Brembach (1976) and Meisner (2001). Given that the modified rays somehow support the transfer of spermatozeugmata or even serve as a true copulatory organ, which is inserted into the female genital opening, the distal parts of the fin rays would have to be stiffened to enable the physical contact. Obviously, this is not the case in *Nomorhamphus*, as the distal segments of fin rays one to five are flexible in most specimens examined.

Additionally, the limited movability of the modified anal-fin rays and the rapidity of the mating process contradict the hypothesis of the andropodium having the function of a true intromittent organ (Brembach, 1976; Greven, 2010; Kelly & Moore, 2016). The greatly elongate genital papilla is more likely to enable the physical contact, whereas the cryptoplica and the modified anal-fin rays could help to orient the genital papilla in the direction of the female during mating, similar to the andropodium of goodeids (Meisner & Burns, 1997a). The limited movability of the genital papilla is probably compensated by the strongly modified anal-fin rays, conducting the spermatozeugmata in the right direction. In contrast, the halfbeak genera *Hemirhamphodon* and *Zenarchopterus* possess a less modified andropodium, as their muscular genital papilla meets the criteria of a true copulatory organ (Greven, 2010). Furthermore, the functional differences of the modified rays are minute between the species, as they are mainly restricted to the shape of the spiculus. According to Arnqvist (1997), in animals exhibiting internal fertilisation, genital morphology of the males usually differs markedly among the species, even if these are quite similar in general morphology. As halfbeaks of the genus *Nomorhamphus* look indeed very similar, and some do occur in sympatry, hybridisation might be avoided by rapid evolution of genitalia, given that females are internally fertilised by the andropodium. The absence of such pronounced differences in male andropodial morphology within the genus weakens the hypothesis of the direct transfer of spermatozeugmata by the modified anal-fin rays.

Conclusions. For determining species-limits within *Nomorhamphus* and its sister clade, general external morphology in combination with the detailed examination of andropodium is useful. Not all species of *Nomorhamphus* endemic to Sulawesi can be determined by andropodial features alone, but the substructure of the modified anal-fin rays allows the classification of distinct groups, exhibiting similar morphology and distributional patterns. The use of this trait is highly recommended, as traditional meristic characters such as counting of scales and fin rays are less informative for morphologically similar species. Besides other findings, the indicated incomplete calcification of the modified fin rays and the resulting flexibility of the whole structure weaken the hypothesis of the andropodium serving as a true intromittent organ.

Material examined. *Nomorhamphus brembachi* – ZMH 7165, holotype, male, 37.6 mm SL; Indonesia, Sulawesi, Southeastern highlands of South-Sulawesi, mountain stream near village Longron, coll. D. Vogt, May 1978; ZMH 7166, paratype, 1 male, 37.0 mm SL; Indonesia, same data as ZMH 7165; MZB 14450, 2 males, 46.0–48.2 mm SL (CT scanned); Indonesia, Sulawesi Selatan, Simbang, Maros, Ta´deang River, destination Samanggi, coll. R. K. Hadiaty, 29 July 2007. Paratypes of *N. ravnaki ravnaki*: ZMH 7159, 1 male, 55.3 mm SL; ZMH 7160, 4 males, 33.7–39.0 mm SL; Indonesia, Sulawesi, highlands of Maros, Ban Timurung, coll. M. Brembach, August 1978. Paratypes of *N. ravnaki australe*: ZMH 7162, 1 male, 55.2 mm SL; ZMH 7163, 14 males, 32.9–56.5 mm SL (1, 33.2 mm SL, cleared and double stained [C&S]); Indonesia, Sulawesi, highlands of Maros, mountain stream near Bossolo, coll. D. Vogt, July 1979. Paratypes of *N. sanussi*: ZMH 7615, 1 male, 44.4 mm SL; ZMH 7616, 10 males, 38.3–49.3 mm SL (1, 40.3 mm SL, C&S); Indonesia, South-Sulawesi, mountain stream near to Segoja, coll. M. Brembach, August 1978.

Nomorhamphus celebensis – ZFMK 49216–49229, 5 males, 28.8–46.5 mm SL (1, 40.7 mm SL, CT scanned; 1, 39.4 mm SL, C&S); Indonesia, Sulawesi, stream crossing road from Tentena southward along East-shore of Lake Poso, 01°48′55.1′S 120°38′03.6′E, coll. F. Herder & & B. Stelbrink, 9 September 2012; ZFMK 49230–49231, 2 males, 34.1–36.3 mm SL, (1, 36.3 mm SL, CT scanned); Indonesia, Sulawesi, Poso river, 01°45.480′S 120°38.738′E, coll. F. Herder et al., 10 September 2012; ZFMK 49232–49235, 1 male, 34.9 mm SL; Indonesia, Sulawesi, Poso river, 01°45.480′S 120° 38.738′E, coll. F. Herder et al., 10 September 2012; ZFMK 49293–49296, 2 males, 38.6–42.3 mm SL; Indonesia, Sulawesi, Poso-mountains near Tentena, Saluopa-waterfall, 01°45.146′S 120°32.498′E, coll. H.-G. Evers et al., 26 September 2010.

Nomorhamphus ebrardtii – ZFMK 49156–49176, 15 males, 42.3–46.7 mm SL (1, 43.0 mm SL, CT scanned; 1, 40.0 mm SL, C&S); Indonesia, Sulawesi Selatan, stream on Malili Road, 2°38.161′S 121°12.920′E, coll. F. Herder et al., 4 May 2004; ZFMK 49287–49292, 2 males, 35.6–36.2 mm SL (1, 36.2 mm SL, CT scanned); Indonesia, Sulawesi Selatan, stream on Malili Road, 2°38.161′S 121°12.920′E, coll. F. Herder et al., 4 May 2004.

Nomorhamphus kolonodalensis – ZFMK 48876–48944, 26 males, 25.9–44.0 mm SL (1, 36.1 mm SL, C&S); Indonesia, Sulawesi Selatan, near Nuha, 2°25.356′S 121°21.426′E, coll. J. Pfaender & J. Schwarzer, 6 December 2002; ZFMK

48945–48959, 5 males, 27.4–48.2 mm SL; Indonesia, Sulawesi Selatan, near Nuha, 2°25.356′S 121°21.426′E, coll. J. Pfaender & J. Schwarzer, 13 June 2010; ZFMK 49103, 1 male, 39.4 mm SL (CT scanned); same data as ZFMK 48945–48959; ZFMK 49104–49118, 7 males, 27.1–42.5 mm SL; Indonesia, Sulawesi Selatan, near Nuha, 2°25.356′S 121°21.426′E, coll. J. Pfaender & J. Schwarzer, 29 April 2004; ZFMK 49237–49253, 7 males, 32.0–46.4 mm SL (1, 40.3 mm SL, CT scanned; 1, 32.0 mm SL, C&S); Indonesia, Sulawesi, North of Matano, 2°23.496′S 121°19.664′E, coll. F. Herder & A. Nolte, 22 March 2011.

Nomorhamphus lanceolatus – MZB 21299, holotype, male, 40.8 mm SL; Indonesia, Sulawesi, Southeast Sulawesi Province, Regency of Kolaka Utara, Wawolambo River, near the bridge on the road, between Kolaka and Kendari, 04°02.516′S 121°42.408′E, coll. R. K. Hadiaty et al., 8 July 2011; MZB 21300, paratypes, 3 males, 30.2–43.0 mm SL (1, 30.2 mm SL, CT scanned); same data as MZB 21299; ZFMK 49526–49529, paratypes, 2 males, 33.7–34.8 mm SL (1, 34.8 mm SL, C&S); same data as MZB 21299; ZMH 25920–25921, paratype, 1 male, 33.6 mm SL; same data as MZB 21299; WFB 3125–3128, paratypes, 2 males, 32.3–33.4 mm SL (1, 32.3 mm SL, CT scanned); same data as MZB 21299.

Nomorhamphus liemi – MZB 14473, 3 males, 41.1–47.5 mm SL (2, 41.1–47.5 mm SL, CT scanned); Indonesia, Sulawesi Selatan, Maros, well of Lampisin, coll. R. K. Hadiaty, 19 July 2007. Paratype of *N. liemi liemi*: ZMH 7618, 1 male, 40.3 mm SL; Indonesia, Sulawesi Selatan, highlands of Maros near Malawa, coll. D. Vogt, August 1978. Paratypes of *N. liemi snijdersi*: ZMH 7156, 1 male, 48.3 mm SL; Indonesia, Sulawesi Selatan, highlands of Maros near Malawa, coll. D. Vogt, August 1978; ZMH 7157, 14 males, 36.6–49.9 mm SL (1, 36.6 mm SL, C&S); Indonesia, South-Sulawesi, highlands of Maros near Malawa, coll. D. Vogt, August 1978.

Nomorhamphus megarrhamphus – ZMH 7152, paralectotype, 1 male, 48.3 mm SL; Indonesia, Sulawesi, Lake Towuti, coll. D. Vogt, July 1981; ZMH 7153, paralectotypes, 24 males, 37.4–47.9 mm SL (2, 43.4–44.0 mm SL, CT scanned; 1, 38.3 mm SL, C&S); same data as ZMH 7152.

Nomorhamphus rex – ZFMK 44944–44955, paratypes, 5 males, 28.9–41.5 mm SL (1, 41.2 mm SL, CT scanned; 1, 35.0 mm SL, C&S); Indonesia, Sulawesi, South Sulawesi Province, Wewu River, a headwater of the Cerekang River drainage west of Lake Matano, tributary at Village Laroeha, small river a few hundred meters upstream of the main river, 2°28.226′S, 121°04.125′E, coll. F. Herder & R. K. Hadiaty, 4 May 2004; ZSM 41743a–d, paratypes, 2 males, 29.2–31.1 mm SL; same data as ZFMK 44944–44955; ZFMK 44956–44961, paratypes, 2 males, 35.7–36.8 mm SL; Indonesia, Sulawesi, South Sulawesi Province, Toletole River at the village of Toletole, at a truck washing place about 150 m upstream of a large river bridge at the road to Wasaponda, 2°31.664′S, 121°06.726′E, coll. F. Herder & R. K. Hadiaty, 4 May 2004; ZFMK 44962–44968, 3 males, 38.0–42.5 mm SL (1,42.5 mm SL, CT scanned; C&S); Indonesia, Sulawesi Selatan, Tana Toraja, in a clearwater pool at an excavation of a small river with unknown name near the village of Tilanga, 3°02.126′S, 119°53.232′E, H.-G. coll. Evers et al., 24 September 2010.

Nomorhamphus sagittarius – MZB 21301, holotype, male, 42.8 mm SL; Indonesia, Sulawesi, Southeast Sulawesi Province, Regency of Kolaka Utara, District Kolaka, Village Ulunggolaka, Mangolo River, coll. R. K. Hadiaty et al., 5 July 2011; MZB 21302, paratype, 1 male, 30.5 mm SL; same data as MZB 21301; MZB 21303, paratypes, 2 males, 33.4–37.1 mm SL; Indonesia, Sulawesi, Mangolo River, about 500 m away from locality of holotype, 03°58.566′S 121°34.055′E, coll. R. K. Hadiaty et al., 5 July 2011; MZB 21304, paratypes, 2 males, 38.0–38.3 mm SL; Indonesia, Sulawesi, Regency of Kolaka Utara, District Kolaka, Village Ulunggolaka, TawoTawo River, 03°59.088′S 121°33.455′E,. coll. R. K. Hadiaty et al., 7 July 2011; MZB 21305, paratype, 1 male, 30.6 mm SL; Indonesia, Sulawesi, Watumbasi River, 03°59.072′S 121°34.107′E, coll. R. K. Hadiaty et al., 7 July 2011; ZFMK 49530, paratype, 1 male, 37.2 mm SL (CT scanned); same data as MZB 21302; ZFMK 49532, paratype, 1 male, 36.7 mm SL (C&S); same data as MZB 21303; ZFMK 49534, paratype, 1 male, 38.9 mm SL; same data as MZB 21304; ZFMK 49536, paratype, 1 male, 39.7 mm SL; same data as MZB 21305; ZMH 25922, paratype, 1 male, 38.1 mm SL; same data as MZB 21304; ZMH 25924, paratype, 1 male, 32.3 mm SL; same data as MZB 21305; WFB 3129, paratype, 1 male, 39.3 mm SL (CT scanned); same data as MZB 21304; WFB 3131, paratype, 1 male, 33.3 mm SL; same data as MZB 21305; MZB 20443, 1 male, 35.2 mm SL (C&S); same data as MZB 21304; MZB 20452, 1 male, 41.2 mm SL (C&S); same data as MZB 21305.

Nomorhamphus towoetii – ZFMK 49254–49281, 8 males, 25.6–40.0 mm SL; Indonesia, Sulawesi, Saluro River, Petea tributary, 02°31.842′S 121°30.006′E, coll. F. Herder, 2 November 2002; ZFMK 49283–49286, 1 male, 40.1 mm SL; Indonesia, Sulawesi, coll. F. Herder, November 2002; ZFMK 48960–49000, 15 males, 25.5–41.6 mm SL (1, 30.5 mm SL, CT scanned; 1, 36.8 mm SL, C&S); Indonesia, Sulawesi, Poso River, 02°32.434′S 121°33.520′E, coll. F. Herder et al., 7 November 2002; ZFMK 49001–49045, 13 males, 29.5–45.9 mm SL; Indonesia, Sulawesi, 02°32.275′S 121°32.281′E, coll. F. Herder et al., 7 November 2002; ZFMK 49046–49077, 15 males, 31.0–44.2 mm SL; Indonesia, Sulawesi, 02°32.243′S 121°31.818′E, coll. F. Herder et al., 7 November 2002; ZFMK 49119–49146, 5 males, 39.4–45.0 mm SL (1, 40.2 mm SL, C&S); Indonesia, Sulawesi, 02°25.320′S 121°13.509′E, coll. F. Herder & R. K. Hadiaty, 4 November 2006; ZFMK 49078–49102, 7 males, 28.3–47.9 mm SL; Indonesia, Sulawesi, Lampesué River, 02°35.358′S 121°40.440′E, coll. F. Herder, 13 November 2006; ZFMK 49147–49155, 2 males, 39.7–44.4 mm SL; Indonesia, Sulawesi, 02°25.320′S 121°13.509′E, coll. F. Herder & R. K. Hadiaty, 14 June 2010; ZFMK 49297–49299, 2 males, 37.6–41.2 mm SL (1, 37.6 mm SL, C&S); Indonesia, Sulawesi, 02°37.899′S 121°12.995′E, Balambano River, coll. H.-G. Evers et al., 28 September 2011; ZFMK 49177–49215, 17 males, 26.9–35.8 mm SL (1, 37.6 mm SL, CT scanned; 1,

34.5 mm SL, C&S); Indonesia, Sulawesi Tengah, Lake Poso, 01°48.117′S 120°38.068′E, coll. F. Herder & J. Pfaender, 8 September 2012.

Nomorhamphus weberi – ZMH 7970, 5 males, 40.2–43.0 mm SL (2, 41.5–42.0 mm SL, CT scanned); Indonesia, Sulawesi, Lake Matano, east of Soroako, coll. M. Kottelat, 19 June 1988.

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