The Gill-Arch Musculature of *Protanguilla*, the Morphologically Most Primitive Eel (Teleostei: Anguilliformes), Compared with That of Other Putatively Primitive Extant Eels and Other Elopomorphs

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The gill-arch musculature and associated aspects of the skeleton of the anguilliforms *Protanguilla*, *Conger*, *Anguilla*, and the synaphobranchids *Synaphobranchus* and *Simenchelys* are described, illustrated, and compared. We identify nine anguilliform synapomorphies, seven myological and two osteological and all but two reported for the first time. We also describe one myological and one osteological synapomorphy of the Anguilliformes minus *Protanguilla*. Our study strongly corroborates the monophyly of the Anguilliformes, which has never been seriously challenged by morphological evidence, and is also supported by molecular analyses. Furthermore, it offers additional morphological support for placing *Protanguilla* as the sister group of all other eels. The condition of many gill-arch skeletal and muscular features are also treated in other elopomorphs and, occasionally, osteoglossomorphs and more primitive actinopterygians. For comparison, we also include the description of the gill-arch muscles of a specialized eel species of the family Serrivomeridae and discuss analyses of its closest family relationships as indicated by several molecular studies.

There is no such thing as good or bad evidence; evidence is evidence.
Donn Eric Rosen in an unrecorded conversation with VGS

JOHNSON et al. (2012) described a new family, genus, and species of eel (Protanguillidae, *Protanguilla*, *P. palau*), which they hypothesized is the sister group of all other eels, both Recent and fossil. Their hypothesis was based on *Protanguilla*'s possession of more plesiomorphic osteological characters than any other eel taxon, and on a cladistic analysis of the mitogenomic characters of *Protanguilla* and representatives of all other families of Recent eels. As noted by Johnson et al., exclusive of *Protanguilla*, "there is no morphology-based consensus of which Recent eels are the most primitive," but "based on gill-arch structure and other osteological features . . . [authors have suggested that] they would most probably be found among the families Synaphobranchidae, Congridae or Anguillidae . . . " This situation persists. In the present study, we examine a soft anatomical system, the gill-arch muscles, for evidence bearing on *Protanguilla*'s anguilliform intra-relationships. Additionally, we comment on other characters and synapomorphies that appear independently in other elopomorphs and less closely related teleostean taxa. For comparison, we include the description of the gill-arch muscles of a specialized eel species of the family Serrivomeridae, which three molecular studies have suggested is closely related to the Anguillidae: Johnson et al. (2012) and Tang and Fielitz (2013), which placed Serrivomeridae and Anguillidae as sister groups, and Inoue et al. (2010), which placed Serrivomeridae + Nemichthyidae as sister to the Anguillidae.

MATERIALS AND METHODS

To study the gill-arch muscles, the entire gill-arch system and some associated bones and muscles, particularly the anterior portion of the sternohyoideus (not a ventral gill-arch muscle)

and its anterior attachments, were removed. Techniques were highly variable and often *ad hoc*. The muscles, many of which are quite delicate, are usually entangled with nerves, blood vessels, and sundry connective tissues that must be removed before study and illustration. In removing these extraneous tissues, occasional damage to some muscles occurred. On the illustrations, damage was adjusted by using information from the same muscle on the opposite side of the specimen, or in a few instances from other specimens that were undamaged in the particular area (but were otherwise in poorer condition than the specimen being illustrated). Most of the muscle damage involved the bilaterally paired ventral and dorsal retractors (VR, DR), which Nelson (1967a) reported are present in all eels. These retractors are anterior continuations of the inner, longitudinal muscle layer of the sphincter oesophagi. Anteroventrally, the VR attaches to the autogenous ventral tooth plate (TP5) and/or the associated fifth ceratobranchial (Cb5). Dorsally, each DR attaches to upper tooth plate 4 (UP4), and perhaps to pharyngobranchial 3. Springer and Johnson (2004; henceforth, S&J) did not treat the dorsal esophageal retractors, and we do not comment on them herein. We devote little attention to the ventral retractors. Posterior to the attachments of the retractors, the outer transverse or circular esophageal muscle layer surrounds the longitudinal layer.

Our descriptions and illustrations of anguilliform gill-arch muscles are mainly restricted to the same eel taxa treated by S&J, who provided descriptions and illustrations of these muscles for three of the four families variously purported to represent the most plesiomorphic anguilliforms (Protanguillidae was unknown at that time). For those three anguilliforms, we reproduce S&J's illustrations of the dorsal gill-arch muscles, with minor changes in labeling, but not the descriptions, for which the reader is referred to S&J. We describe and illustrate the ventral gill-arch muscles for all these taxa, as well as both the dorsal and ventral gill-arch muscles of two additional genera, *Protanguilla* (Protanguillidae), described in 2012, and *Simenchelys* (Synaphobranchidae), not treated by S&J. Additionally, we provide a complete description of the gill-arch musculature of a specialized eel,
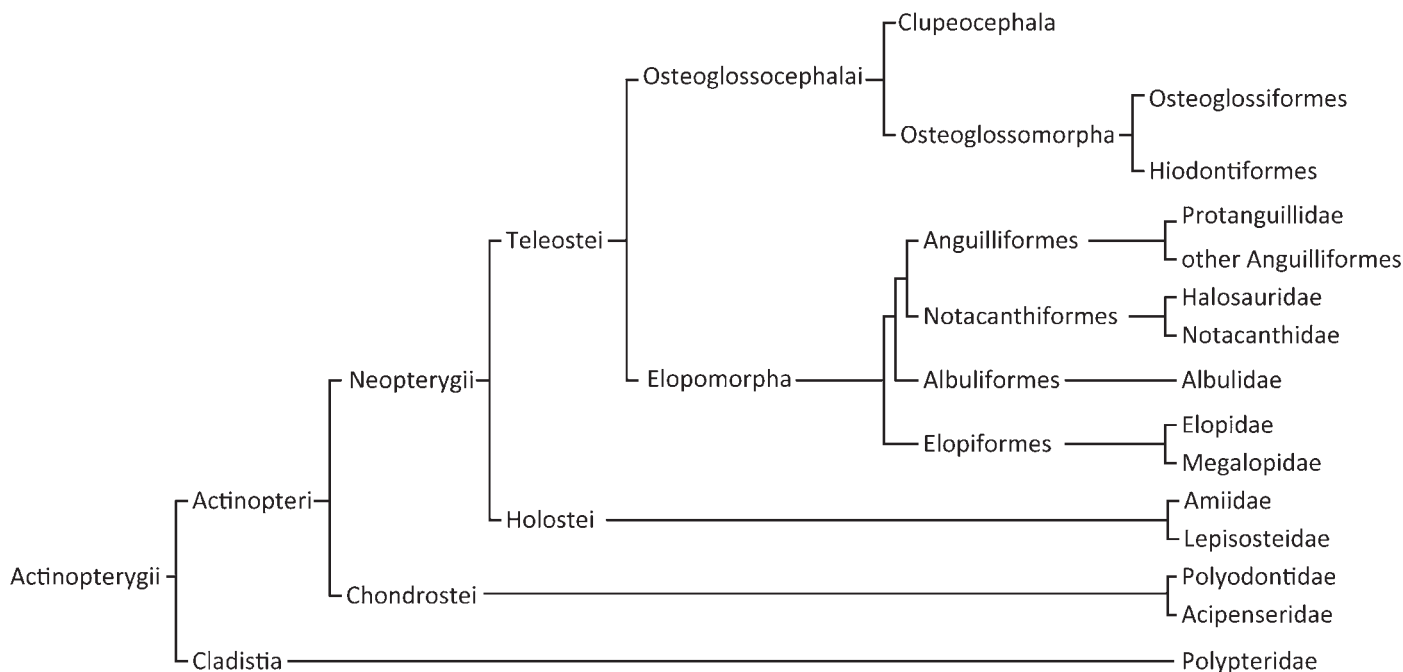
Fig. 1. Cladogram showing suprageneric taxa referred to in the present study extracted from the molecular study of Betancur et al. (2013), of which the lower part agrees with morphological evidence of Grande (2010) and the upper part with Arratia (1999, 2000a, 2000b, 2010, etc.). For clupeocephalan intrarelationships see Springer and Johnson (2004:fig. 3).

Serrivomer beanii Gill and Ryder. Descriptions or indications of selected gill-arch muscles are also provided for various anguilliform and non-anguilliform elopomorph taxa we examined. The descriptions and illustrations of the dorsal gill-arch musculature of many of the non-anguilliform elopomorph taxa are available in S&J.

We base our discussions on an abbreviated molecular phylogeny of actinopterygians as hypothesized by Betancur et al. (2013), expanded to include more clades within its proposed basal clades (Fig. 1).

A summary of the relevant dorsal and ventral gill-arch muscles of all the main anguilliform taxa we treat and an example representing each of the main non-anguilliform elopomorph clades are provided in Table 1.

Institutional abbreviations follow Sabaj Pérez (2014).

Specimens of anguilliforms are listed at the beginning of each species description. With a few noted exceptions, information on the gill-arch muscles of *Moringua*, *Kaupichthys*, *Uropterygius*, and *Gymnothorax* are derived from Nelson (1967a). Some partial descriptions are also presented for the gill-arch muscles and/or skeleton for which the gill-arch muscles are not illustrated. These include: *Ophichthus puncticeps* (Kaup), Ophicthidae, USNM 431417, ca. 600 mm TL; *Muraenesox cinereus* (Forsskal), Muraenesocidae, USNM 431418, ca. 540 mm TL; and *Hoplunnis tenuis* Ginsburg, Nettastomatidae, USNM 431416, ca. 530 mm TL.

Specimens of non-anguilliform elopomorphs are as follows (taxa described and illustrated in S&J are indicated in parentheses: *Notacanthus chemnitzi* Bloch, USNM 214342 (S&J), USNM 214340, ca. 345 SL, USNM 214341, ca. 275 SL; *Polyacanthonotus challengeri* (Bloch), USNM 263242, ca. 435 mm TL; *Lipogenys gillii* Goode and Bean, USNM 358858, 297 mm SL; MCZ 38072, ca. 192 mm SL; *Albula vulpes*?, USNM 247511 (S&J); *Pterothrissus belloci* Cadenat, USNM 304454, 180 mm SL (S&J used a different species of *Pterothrissus*); *Aldrovandia affinis* (Gunther), USNM 319707 (S&J); *Elops smithi* McBride et al., 2010, USNM 121694 (same specimen

indicated as *E. saurus* in S&J); *Megalops cyprinoides* (Broussonet), USNM 350468 (erroneously indicated in S&J text as 350458).

ANATOMICAL ABBREVIATIONS WITH DEFINITIONS AND DISCUSSIONS

Abbreviations for names of muscles and skeletal elements variously and occasionally extensively described and annotated follow (parenthetical abbreviations are equivalents used by Nelson, 1966a, 1967a). Among the annotations, we indicate the most strongly supported synapomorphies for dorsal gill-arch elements derived from optimizing characters on the cladogram in Figure 1. Many of these correspond to those hypothesized by S&J (2004:fig. 3), which were based on a different, exclusively morphology-based cladogram compiled from the literature (see S&J, 2004:16–18, for a discussion of the various sources used to construct that cladogram). Anguilliform synapomorphies for some ventral gill-arch muscles are also hypothesized based either on our own observations or on published information.

AC4—accessory element (cartilage) at distal end of ceratobranchial 4. Traditionally, this cartilage has been treated as epibranchial 5 (e.g., S&J), but Carvalho et al. (2013) clearly demonstrated that in teleosts the cartilage develops from the distal cartilaginous end of ceratobranchial 4 and has no association with the fifth gill arch. All non-anguilliform Elopomorpha, except the albulid *Albula*, examined by S&J, and the highly specialized notacanthid *Lipogenys* (Kanehira et al., 2012) have AC4. The absence of AC4 is synapomorphic for anguilliforms, and we assume that AC4 has been independently lost in *Albula* and *Lipogenys*.

Ad—adductor; a gill-arch muscle, here applied, with two exceptions, to one attaching the anterior surface of an epibranchial to the anterior surface of its associated ceratobranchial. Ad4 and Ad5 are two of the most common

Table 1. Distribution of 38 muscle and three skeletal gill-arch characters in six taxa of eels and six taxa of other elopomorphs: p = present; – = absent; c = cartilaginous; o = bony; 1, 2 = number of PCls on each side. SPh presence indicates presumed fusion of R3+R4+R4Cm. Except for R1, autapomorphies of *Serrivomer* are not included.

Dorsal muscles	LE1–4	Ll1&2	Ll3	TD on Pb3	TD on Eb4	TD on UP3	TD on UP4	OD3	OD4	ER	MPb2-Eb1	MPb2-Eb2	RecD1	RecD2	RecD3	RecD4	Ad1–3	Ad4
Eels																		
Protanguilla	p	1&2	–	p	–	–	p	–	p	p	p	–	p	p	p	p	–	p
Conger	p	1&2	–	p	p	–	–	–	p	p	p	–	–	p	p	–	–	p
Anguilla	p	1&2	–	p	p	p	p	p	p	p	p	–	p	p	p	–	1&2	p
Synaphobranchus	p	1&2	–	p	–	p	p	p	p	p	–	p	–	p	–	–	–	p
Simenchelys	p	1&2	–	p	–	–	–	–	p	p	p	–	–	–	p	–	p	p
Serrivomer	p	1&2	–	p	–	–	p	–	–	–	p	–	–	–	p	–	–	p
Other elopomorphs																		
Notocanthus	p[1]	1&2	–	p	p	–	–	–	p	–	–	–	–	–	p	–	p	p
Aldrovandia	p	1&2	p	p	–	–	–	p	p	–	–	–	–	–	p	–	–	p
Albula	p	1&2	p	p	–	–	p	–	p	p	–	–	–	–	–	–	–	p
Pterothrissus	p	1&2	p	p	–	–	–	–	p	p	–	–	–	–	–	–	–	p
Elops	p	1&2	p	p	p	–	–	p	p	p	–	–	–	–	–	–	–	p
Megalops	p	1	p	p	p	–	–	p	p	p	–	–	–	–	–	–	–	p

Ventral muscles	R1	R2	R3	R4	R4Cm	SPh	ObV1	ObV2	ObV3	PCl	Ad5	TV4	TV5	RecCom	AC4[2]	Hb3[2]	[2]Bb3,Bb4, Hb3 complex[3]
Eels																	
Protanguilla	–	–	p	p	–	–	p	p	–	1	p	p	p	–	–	c	p
Conger	–	–	p	p	p	–	p	p	p	1	p	p	p	–	–	c	–
Anguilla	–	p	p	p	p	–	p	p	p	1	p	p	p	–	–	c	–
Synaphobranchus	–	–	p	p	p	p	p	p	–	1	–	p	p	–	–	c	–
Simenchelys	–	–	p	p	p	p	–	–	–	1	p	p	p	–	–	c	–
Serrivomer	p	p	p	p	p	–	p	p	p	1	p	p	?	–	–	c	–
Other elopomorphs																	
Notocanthus	–	–	–	–	–	–	p	p	p	1	p	p	p	p	p	o	p
Aldrovandia	–	–	–	–	–	–	p	p	p	2	p	p	p	p	p	o	p
Albula	–	–	–	–	–	–	p	p	p	2	p	p	p	p	–	o	–
Pterothrissus	–	–	–	–	–	–	p	p	p	2	p	p	p	p	p	o	p
Elops	–	–	–	–	–	–	p	p	p	2	p	p	p	p	p	o	p
Megalops	–	–	–	–	–	–	p	p	p	2	p	p	p	p	p	o	p

[1] See discussion under LE in abbreviations section.

[2] Skeletal character.

[3] The primitive teleostean configuration of BB3, BB4, and Hb3 wherein the Hb3s have narrowed extensions that extend well forward along each side of the well-developed Bb3, which articulates tightly with a well-developed Bb4 and may have a posterior "tail" that extends below Bb4.

muscles in actinopterygian fishes. In teleosts, Ad4 attaches the posterior surface of Eb4 to Cb4 and Ad5 attaches Cb5, variously, to Cb4, AC4 (prior to Carvalho et al. [2013] believed to be Eb5), ER, OP, and SO. Neither of these two muscles appears to be serially homologous with Ad1–3 or 4′, which attach to the anterior surfaces of their respective Cb and Eb. Although it appears that Ad4′, which is known only in notacanthids, should be designated as Ad4, we prefer to maintain the traditional assignment of Ad4, as described above. As considered in our study, Ad1–3 are known only for *Simenchelys* and notacanthids, Ad2 and 3 are present in *Anguilla*, and Ad4′ is only known in notacanthids. None of the other eels and elopomorphs we examined have Ad1, 2, or 3, which are also lacking in all osteoglossomorphs.

AntCh—anterior ceratohyal.

Bb (B)—basibranchial. With the exception of some ostariophysans in which it is ossified, Bb4 is cartilaginous or absent in fishes, including elopomorphs.

Cb (C)—ceratobranchial.

CT—connective tissue; used to indicate non-muscular tissue, the exact nature of which was not established.

DR (DR)—dorsal retractor; present in all eels; longitudinal SO muscle fibers extending anteriorly from esophageal wall and attaching to UP4 and various other posteriorly located dorsal gill-arch skeletal elements; usually not illustrated or reported. Its distribution in non-anguilliforms was not investigated. See also DR in *Simenchelys*.

Eb (E)—epibranchial.

ER—esophageal raphe; a fine line of connective tissue, or septum, separating the ventral end of OP from Ad5 and/or SO.

GFM—gill filament muscle. We do not discuss or illustrate GFMs, and mention them here only because in all but two of the many instances where S&J indicated GFMs in their muscle descriptions and species illustrations, they should have indicated Ads. S&J's indications of GFMs in *Scomber* and *Novumbra* should have been indicated as RecDs (see also Ad above).

Hb (H)—hypobranchial; Hb3 is partially or mostly bony in Elopomorpha (Nelson, 1966b; Kanehira et al., 2012), except anguilliforms, in which it is synapomorphically entirely cartilaginous or absent (Nelson, 1966a:table 1; not noted in Johnson et al., 2012).

Hyh—hypohyal. Most eels have one or no Hyh on each side; only *Simencheleys* has two. De Pinna (1996) summarized the distribution of hypohyals in fishes, ''In sarcopterygians and basal actinopterygians, the hyoid arch has a single hypohyal. Such is the condition in *Polypterus* . . . , chondrosteans . . . lepisosteids . . . , and various paleonisciform fossils . . . '' He indicated that there was a minor question about the apparent single hypohyal in *Amia*, but there is only one in specimens we have seen. De Pinna went on to state that in nearly all teleosts, Recent and fossil, there are two hypohyals, and that two hypohyals is a teleostean synapomorphy.

LE (EL)—levator externus; dorsal gill-arch muscle originating on the cranium (exact position not recorded) and inserting on an epibranchial, e.g., LE2 inserts on Eb2. LE1–4 are present in all elopomorphs. S&J (text and plate volumes) indicated that LE4 is absent in *Notacanthus*. On their plate 19, they label a ''ligament'' attaching to Eb4. Additional dissections indicate that appressed to LE3 there is a very fine muscular LE4 with an extremely long and very fine tendon extending posteriorly and inserting on Eb4 dorsally. The muscle is easily overlooked and the tendon is easily broken.

We presume the ligament noted by S&J is a tendinous remnant of the insertion of LE4. *Polyacanthonotus* is similar to *Notacanthus* except that LE4 is all muscular.

LI (IL)—levator internus; dorsal gill-arch muscle originating on the cranium (exact position not recorded) and inserting variously on one or more Pbs (excluding Pb1, the absence of which is an anguilliform synapomorphy) and/or associated tooth plates. Internal levators LI1 and LI2 first appear in, and are thus synapomorphic for Holostei, and LI3 is a synapomorphy of Teleostei (see S&J:71 for further discussion). It first appears together with Pb4 in Elopomorpha, and is present in all major pre-ctenosquamate teleost clades. It is absent synapomorphically in Anguilliformes and has been lost independently in the notacanthids *Notacanthus, Polyacanthonotus*, and probably *Lipogenys*, which lacks Pb4.

MCb5-TP5—musculus ceratobranchialis 5-laminalis dentalis 5 (not illustrated); small ventral gill-arch muscle attaching Cb5 dorso-anteromedially and broadly to associated TP5 posteriorly; present only in *Protanguilla*; possibly represents a disjunct part of the ventral retractor.

MPb2-Eb1 (AO)—musculus pharyngobranchialis 2-epibranchialis 1; small dorsal gill-arch muscle attaching Pb2 to Eb1. This muscle is found only in anguilliforms and mormyrid osteoglossiforms, and is separately synapomorphic for each of these two groups. It is absent in *Synaphobranchus*, in which Pb2 has been reduced to a small cartilage and has possibly been replaced by MPb2-Eb2 (q.v.).

MPb2-Eb2—musculus pharyngobranchialis 2-epibranchialis 2; small dorsal gill-arch muscle attaching Pb2 to Eb2. Among elopomorphs, we found this muscle only in *Synaphobranchus*, where it is possibly a replacement for MPb2-Eb1 (q.v.). Aside from its unique attachment to Eb2, the muscle attaches on the ventral surfaces of the skeletal elements, whereas the attachments of MPb2-Eb1 are on the dorsal surfaces.

MUP4-Eb4—musculus laminalis pharyngobranchialis dentalis 4-epibranchialis 4; dorsal gill-arch muscle attaching UP4 to Eb4; only noted in *Conger*, possibly represents an extension of the dorsal retractor.

OD (SO)—obliquus dorsalis; dorsal gill-arch muscle originating on Pb3 and inserting on Eb3 (OD3) and/or Eb4 (OD3-4 [a fusion], OD4, OD4′). OD3 is present in both Osteoglossomorpha and Elopomorpha, and is, thus, synapomorphic for Teleostei.

ObV (O)—obliquus ventralis; ventral gill-arch muscle attaching the ceratobranchial of a gill arch to its associated hypobranchial. ObV1–3 are present in fishes at least as phylogenetically primitive as the halecomorph *Amia*. ObV 1–3 are present in *Conger*, *Anguilla*, *Moringua*, and *Serrivomer*; only ObV1 and 2 are present in *Protanguilla* and *Synaphobranchus*; and all are absent in *Simenchelys* and, according to Nelson (1967a:table 1), *Kaupichthys*, *Uropterygius*, and *Gymnothorax*.

OP (PO)—obliquus posterior; dorsal gill-arch muscle originating on the posterior surface of Cb4 and extending ventrally, variously ending at the esophageal raphe (ER) with the sphincter esophagi (SO), and/or Ad5, or inserting on Cb5. OP first appears in Holostei (Amiidae [questionably in Lepisosteidae; see S&J:24]) and is usually present in most Teleostei (see S&J:table 1 for pre-Acanthomorpha; see Springer and Orrell [2004:239, characters 25 and 26 for character states of OP, and table 12 for their distribution in Acanthomorpha]).

PCl—pharyngoclavicularis; ventral gill-arch muscle. Fishes normally have two PCls on each side (an internus, and an externus), both of which originate on the cleithrum and insert on Cb5 and frequently, if present, its associated tooth plate (TP5). Among the Elopomorpha, anguilliforms have only one PCl on each side, which is probably an anguilliform synapomorphy; however, among the Notacanthiformes, which consists of Notacanthidae + Halosauridae, sister group of the Anguilliformes, each of the three genera of Notacanthidae also have only one PCl. The PCl of *Notacanthus* and *Polyacanthonotus* originates, as usual, on the cleithrum, but we were unable to establish that PCl originates on the cleithrum in the highly specialized *Lipogenys*. In *Lipogenys* PCl appears to be represented by a well-developed pair of muscles that inserts tendinously and ventrally on its unusually well-developed cartilaginous Bb4. Some of the insertion fibers appear to attach to the small, weakly developed Cb5, which lacks a tooth plate, but is positioned close to Bb4. For an extended discussion of PCl in basal Actinopterygii see S&J:22 (as PC, PCl, PCE).

R (R)—rectus ventralis; ventral gill-arch muscle extending from the Cb of one gill arch to the Hb of the preceding gill arch; numbered based on that of the originating ceratobranchial (e.g., R2 originates on Cb2 and inserts on Hb1). Within Elopomorpha, presence of recti ventrales appears to be synapomorphic for anguilliforms (note: Nelson's [1966b:fig. 83; 1967b:table 1] R4 in *Elops* is our RecCom). R2–R4 are present in *Anguilla*, only R3 and R4 in *Protanguilla*, *Conger*, and synaphobranchids, and only R4 in *Moringua* and *Kaupichthys* (Nelson, 1967a), and none are present in muraenids (Nelson, 1967a). Remarkably, R1 is present in *Serrivomer*. As there is no Hb anterior to Cb1, the insertion of R1 in *Serrivomer* is on the anterolateralmost surface of the anterior ceratohyal. We also note that R4 (but not R2 or R3) is present in several Osteoglossomorpha (Greenwood, 1971) and is probably synapomorphic for that clade.

R4Cm (RC)—rectus ventralis 4 communis; an anteriorly elongate ventral gill-arch muscle posteriorly attaching on Cb4, usually together with the much shorter dorsally positioned R4, and extending anteriorly to a gill-arch element anterior to Hb3, e.g., Hb2, Hb1, urohyal. Within the Elopomorpha, R4Cm is absent in *Protanguilla*, but is present in the putatively plesiomorphic anguilliform families Congridae, Anguillidae, and Synaphobranchidae, and the more specialized Moringuidae, Chlopsidae, and Serrivomeridae. R4Cm is, thus, synapomorphic for eels other than Protanguillidae, and its absence in *Protanguilla* supports the position of *Protanguilla* as the sister group of all other eels. R4Cm was apparently lost secondarily in the highly specialized muraenids.

Nelson (1967a:fig. 5) indicated that the RC (our R4Cm) and R4 origins are well separated on Cb4 in the moringuid *Moringua javanica*. We confirmed this condition, which may be unique within eels, in another specimen (USNM 315551) of *Moringua* sp. from Taiwan. Nelson (1967a:fig. 7) also illustrated the apparently more typical condition of R4 in the chlopsid *Kaupichthys diodontus*, which we also found in a different specimen (USNM 141257) of the same species. Additionally, we found the typical condition for R4 and R4Cm in the serrivomerid *Serrivomer beanii*.

Interestingly, Greenwood (1971, his rectus communis [RC] = our R4Cm) described the typically anguilliform R4Cm-R4 arrangement in the osteoglossomorph *Hiodon* (also seen by us in USNM 350554) and *Pantodon* (not

examined by us). In *Heterotis*, he reported what might be the typical arrangement, but noted that a ligament replaced R4. Among the several other Osteoglossomorpha he examined, Greenwood indicated that most have only R4Cm, the remaining, only R4. In any event, as in eels, all of these muscles originate on Cb4, with R4 extending anteriorly only to Hb3 and R4Cm extending more anteriorly. See also discussion of R4Cm versus RecCom under RecCom.

RecCom (R4, RC in part)—rectus communis; elongate ventral gill-arch muscle that first appears in the halecomorph *Amia*, in which it begins posteriorly as a long tendon extending anteriorly from Cb 5, becoming strongly muscular, joining, or not, a smaller dorsally positioned muscle [R4] on Cb4 and attaching on Hb3 (Allis, 1897:674, as *obliqus ventralis*, IV^2, fig. 47). It is a halecostome synapomorphy and is present in its primitive state in all non-anguilliform elopomorphs except Albulidae and Pterothrissidae, in which it lacks attachment to Cb5 and is only muscular on Cb4. We early debated treating our R4Cm in anguilliforms as a modified RC (which it may be) that had undergone two or three modifications: loss of a tendinous connection with Cb5, consequent muscular attachment to Cb4, and increased its anterior attachment to a skeletal element anterior to Hb3. The presence of our R4, however, which only differs from RC in having lost the tendinous connection to Cb5, particularly evidenced in *Moringua*, convinced us about our parsimoniously influenced identifications of the two muscles. Our abbreviation, R4Cm, alludes to the possibility that it is a RecCom derivative. The presence and state of R4Cm, whether considered as a variant RC or a new muscle, is a teleostean synapomorphy, and its presence in anguilliforms and osteoglossomorphs is separately synapomorphic for each group.

RecD (IO)—rectus dorsalis; dorsal gill-arch muscle usually originating on an epibranchial and attaching to the preceding epibranchial; numbered based on that of the originating epibranchial (e.g., RecD3 originates on Eb3 and inserts on Eb2). In *Protanguilla*, the only eel with an unequivocal identifiable RecD4, the muscle, unexpectedly, attaches Eb4 to Eb2. Winterbottom (1974:259), using the plural form, first applied the name recti dorsales to these muscles, for which previous authors had used a variety of names. Winterbottom noted the variable occurrence of these muscles among teleosts. See also S&J:217 for discussion of previously published erroneous indications of attachments of RecDs in callionymids.

S&J (2004:72), using a more extensive actinopterygian, morphology-based cladogram (their fig. 3) than that of our Figure 1, optimized dorsal gill-arch muscle states for elopomorphs that included most of the taxa we examined for our study (notably lacking were *Protanguilla*, *Simenchelys*, and *Serrivomer*). In agreement with our findings, S&J reported that RecD2 is a synapomorphy of Anguilliformes (and also separately, and at different levels, a synapomorphy of S&J's Osteoglossiformes and Cypriniformes). We found the presence of one or more RecDs to be synapomorphic for Anguilliformes within the Elopomorpha. The absence of RecDs in *Simenchelys* is a secondary loss. Several eels, including *Protanguilla*, have RecD1. As there is no epibranchial anterior to Eb1, a different element must serve in its place. Nelson (1967a) reported the presence of RecD1 in Anguillidae, Moringuidae, Chlopsidae, and Muraenidae, but he did not describe its anterior attachment in any of the four taxa. S&J (2004:39) erroneously described RecD1 of *Anguilla*

as ending tendinously anteriorly in the connective tissue of the roof of the mouth. As first reported correctly by Dietz (1912:30, 32, as interarcuales dorsalis, abbreviated as ''id'') for *Anguilla*, RecD1 attaches on the dorso-medial surface of the posterior ceratohyal. Nelson (1967a:fig. 6) only illustrated a single muscle, in addition to LE1, extending anteriorly from Eb1 in each of the four taxa he indicated as having RecD1. We found, however, that in *Moringua* sp. (USNM 315551, 810 mm TL), in addition to LE1, there are two slender muscles originating at the lateral end of Eb1 and extending far anteriorly, as does RecD1 in *Anguilla*. The lateralmost of these passes lateral to the dorsomedial tip of the posterior ceratohyal and appears to dissipate into connective tissue anterior to that point. The medialmost inserts by a tendinous sheet on the medial surface of the opercle. In the chlopsid *Kaupichthys diodontus* (USNM 141258, 109 mm TL), we found RecD1 originating on the joint between Eb1 and Cb1, but mostly on Cb1, and extending to the dorsalmost area of the posterior ceratohyal, similar to *Anguilla*. We examined two specimens of the muraenid *Gymnothorax rueppelliae* (USNM 141579, ca. 210 and ca. 400 mm TL). In the smaller specimen we found a single, weakly developed muscle originating laterally in the joint between Eb1 and Cb1 and extending ventrally and dissipating among the ventral gill-arch muscles. In the larger specimen, there is a fan of well-developed muscles originating at the Eb1-Cb1 joint and continuing ventrally along Cb1, with various branches questionably attaching to the hyoid apparatus or dissipating in various antero-ventral directions among the ventral gill arch musculature. Because eels are unusual in the extreme posterior position of their gill arches, we expect there may be considerable variation in the presence, absence, and insertion of RecD1-like muscles, the variations of which are beyond the scope of our study.

SO—sphincter oesophagi; muscle associated with the tubular portion of the digestive tract that begins just posterior to the gill arches. It comprises an outer layer of transverse or circular muscle fibers surrounding an inner layer of longitudinal muscles fibers. At least in eels (all according to Nelson, 1967a), longitudinal muscle fibers extend anteriorly from the anterior end of SO and attach to the posteriormost portions of the gill-arch skeleton. Nelson termed these dorsal and ventral retractors (DR, VR). We rarely mention these, which may appear simply as the basis for attaching SO to the gill arches.

SPh—subpharyngealis; longitudinal ventral gill-arch muscle on dorsal surface of ventral gill arches, variously consisting of partial or unknown complete fusions of various ventral gill-arch muscles. It originates on Cb4, and Nelson (1967a:362) suggested that it replaced the recti and obliqui. There is evidence in *Synaphobranchus* that SPh incorporates parts of R3, R4, and R4Cm, but not ObV1 and Obv2, which are distinct; the contribution, if any, of ObV3, which is absent in *Synaphobranchus*, is unknown.

Nelson did not report the anterior insertion of SPh for any of the four eel families he indicated that have it: Synaphobranchidae, Moringuidae, Chlopsidae, and Muraenidae. In *Synaphobranchus*, SPh inserts on the single hypohyal. Jaquet (1920) indicated that it attached on the hyoid arch in Simenchelys, and his illustration shows it attaching at the anterior end, which could be the hypohyals (*Simenchelys* is the only Recent eel with two hypohyals on each hyoid arch). In addition to Protanguillidae, Congridae, and Anguillidae, SPh is absent in Serrivomeridae and (one specimen of each examined) Muraenesocidae, Ophichthidae, and Nettastomatidae. More eel families should be examined for the presence of SPh, but we suggest that SPh may be synapomorphic for a large clade of anguilliform families. In this regard, we mention that recent analyses based on molecular data (e.g., Inoue et al., 2010; Johnson et al., 2012; Tang and Fielitz, 2013) proposed that Synaphobranchidae is either the sister group of, or closely related to, the Protanguillidae, which lacks SPh, and is morphologically the sister group of all other eels.

TD (TD)—transversus dorsalis, a muscle spanning the contralateral elements of the dorsal gill-arch skeleton, usually reported according to the elements it attaches to. See TEb2, TPb3, etc. An attachment of the transversus dorsalis anterior to Eb4 first appears in, and is thus synapomorphic for Neopterygii.

TEb2—transversus epibranchialis 2; dorsal gill-arch muscle connecting right and left Eb2s. An attachment of the transversus dorsalis that includes Eb2 first appears in the Elopomorpha, but only in *Notacanthus*. The attachment is spotty and rare in other pre-acanthmorphs, except for some Osteoglossomorpha (not including *Hiodon*) and Otophysi (but not including cyprinoids). The attachment becomes common (almost universal) in Neoteleostei and Acanthomorpha, with the notable exception of atherinomorphs (see S&J:tables 4 and 9, and note the following corrections in the caption for their table 4: ''synapomorphies (30–40)'' should be ''synapomorphies (31–35)''; ''partly on Pb43'' should be ''partly on Pb4'').

TP3—tooth plate associated with Cb3 in *Synaphobranchus*. Johnson et al. (2012), in comparing the unique plesiomorphic presence of gill rakers in *Protanguilla* with their absence in other eels, observed that small tooth plates are near the cerato-epibranchial junction of the first three arches of *Synaphobranchus* and *Kaupichthys*. The implication was, correctly, that these small (actually tiny) tooth plates are specializations not comparable to gill rakers, but additional implications were that these small plates are not present in other eels and that other much larger tooth plates on the arches are also absent. We noted these circumstances after cleaning the gill arches of most of the eel specimens we studied, but found the tiny tooth plates, as Johnson et al. (2012) described on the first three arches of *Anguilla marmorata*, and we also found a moderately large to very large tooth plate (not illustrated) on Cb3 of *Synaphobranchus*. Nelson (1966a, 1967a) neither illustrated nor mentioned the tiny or larger tooth plates in any eel, and we know of no other report of the existence of these tooth plates. It is possible that the tiny tooth plates may also be present in other eels than those we report. That they are not homologs of true gill rakers is supported by our observation that they occur in addition to the double rows of toothed gill rakers on Cb1–4 in *Elops* and *Megalops*.

TP5—tooth plate associated with Cb5. Nelson (1966a) indicated that all eels, except those of the genus *Synaphobranchus*, have a single, autogenous, tooth plate associated with Cb5. Nelson illustrated and described the gill-arch skeleton of *Synaphobranchus affinis* Günther, the only species of the genus he listed in his material, as having four autogenous tooth plates associated with each Cb5. Both of our specimens of *Synaphobranchus* appear to be identifiable as *S. kaupii* Smith, and have only one large tooth plate, equal in area to the four tooth plates Nelson illustrated for *S.*

affinis, associated with each Cb5. Nelson considered the multiple tooth plates important because they appear to be a primitive feature found in other lower teleosts, such as *Hiodon*, *Osteoglossum*, *Elops*, and *Pterothrissus*, ''but are generally unknown in other teleosts'' he examined. He mentioned that *Conger* initially has a pair of tooth plates associated with Cb5, but that these fuse during ontogeny. Whether the tooth plate of *S. kaupii* represents an ontogenetic fusion of several independent tooth plates requires additional study. Robins (1971:fig. 10) described and illustrated the lower pharyngeal tooth plates in four species of synaphobranchids. In *Synaphobranchus affinis* she reported that the tooth plates are ''multiple, but the number of elements is not constant.'' In her two specimens, she stated there were three ''elements'' on each side in one specimen and three on one side and four on the other side in the other specimen. Her illustration, however, indicates two plates on one side and three on the other. For *S. oregoni* she stated, and illustrated, that there is only one plate on each side, but that each plate is ''deeply incised at several points.'' For *S. kaupii* she described and illustrated a single large plate on each side with no indication of incision. Finally, for *Iliophis brunneus*, she stated that there is one plate on each side, each with an eroded outline on its medial margin. Obviously, the number of tooth plates is variable, and possibly the variation is ontogenetically influenced.

TPb3—transversus pharyngobranchialis 3; dorsal gill-arch muscle connecting right and left Pb3s. An attachment of the transversus dorsalis that includes Pb3 first appears in Holostei, and is almost universally present in preacanthomorphs. It is also very common in acanthomorphs.

TPb3-UP3-UP4—transversus pharyngobranchialis 3-laminalis dentalis 3-laminalis dentalis 4; dorsal gill-arch muscle connecting right and left Pb3s, UP3s, and UP4s. An attachment of the transversus dorsalis that includes either UP3 or UP4 is extremely uncommon in preacanthomorphs, except for some anguilliforms. Attachment to UP3 is absent in acanthomorphs, and attachment to UP4 is rare.

TPb3-UP3-UP4-Eb4—transversus pharyngobranchialis 3-laminalis dentalis 3-laminalis dentalis 4-epibranchialis 4; transverse dorsal gill-arch muscle connecting right and left Pb3s, UP3s, UP4s, and Eb4s. An attachment of the transversus dorsalis that includes Eb4 first appears in Chondrostei and is commonly present in preacanthomorphs. It has a spotty occurrence in acanthomorphs but is common in pharyngognaths and clinids.

TPb3-UP4 (S)—transversus pharyngobranchialis 3-laminalis dentalis 4; transverse dorsal gill-arch muscle connecting right and left Pb3s and UP4s.

TPb4-Eb4 (S)—transversus pharyngobranchialis 4-epibranchialis 4; transverse dorsal gill-arch muscle connecting right and left Eb4s.

TV4 (AT)—transversus ventralis anterior; transverse dorsal gill-arch muscle connecting right and left Cb4s.

TV5 (PT)—transversus ventralis posterior; transverse dorsal gill-arch muscle connecting right and left Cb5s; often continuous posteriorly with SO, but distinguished from SO in having a median raphe that occasionally continues anteriorly as a slender tendon.

UP3 (UP3)—tooth plate associated with Pb3.

UP4 (UP4)—tooth plate associated with Pb4.

VR (VR)—ventral retractor; longitudinal SO muscle fibers extending anteriorly and attaching to Cb5 and, variously,

TP5; usually not investigated or illustrated; according to Nelson (1967a), it is present in all eels.

DESCRIPTIONS OF BRANCHIAL MUSCULATURE IN ANGUILLIFORM TAXA

Protanguillidae

Protanguilla palau Johnson et al.
Figures 2 and 3

Material.—Mainly described and illustrated based on USNM 396051, 156 mm TL; additional material, CBM-ZF 12279, 73.8 mm TL.

Dorsal gill-arch muscles

LE1 inserts on lateral one-third of Eb1 dorsoposteriorly; ventrolateral edge of insertion is medial to the medial edge of RecD1.

LE2 inserts on lateral one-third of Eb2 dorsoposteriorly; ventrolateral edge of insertion is adjacent to the medial edge of RecD2 on left side, slightly separated from RecD2 on right side.

LE3 very slender, inserts finely on lateral one-third of Eb3 dorsoposteriorly; right-side insertion on edge of Eb3 that abuts similar Eb4 edge and adjacent to medial edge of RecD3; left-side insertion similar, but origin of RecD3 on anterior edge of Eb3 well removed from LE3 insertion.

LE4 very slender, inserts very finely on lateral one-fourth of Eb4 near posteromedial edge of RecD4.

LI1 inserts on expanded dorsoanteriormost Pb2 surface that meets medial end of Eb1.

LI2 relatively large, extends posteroventrally from its origin and passes ventral to OD4, forming a shallow bifurcate insertion with the medial branch inserting on Pb3 dorsoposterolaterally and a lateral branch on UP4 dorsoanterolaterally.

TD comprises TPb3-UP4, which attaches anteriorly to the dorsoanterior end of each Pb3 and forms a thin transverse muscle layer for most of its length; posteriorly, the muscle is continuous seamlessly with SO; at about a horizontal between the posteromedialmost edge of each Eb4, a small strap of transverse muscle on each side delaminates ventrally and attaches on its respective side to the dorsolateral surface of UP4.

MPb2-Eb1 extends anteriorly along the dorsal half of the bony surface of Pb2 to the medial end of Eb.1

OD3 absent.

OD4 originates on Pb3 dorsoanterolaterally, meeting anteriormost attachment of TPb3-UP4, and extending posterolaterally and inserts on mid-dorsal edge of Eb4 that impinges on Eb3.

RecD1 originates on posterolateral edge of Eb1, its medial edge impinging on ventrolateral edge of LE1 insertion. Its insertion was lost during removal of the gill arches (the muscle was possibly attached to the dorsal tip of the posterior ceratohyal, as it is in *Anguilla*).

RecD2 originates along posterolateralmost edge of Eb2, posteriorly meeting combined insertions of RecD3 and 4 and medially meeting lateral edge of LE2 insertion on left side, but somewhat separated from LE2 insertion on right side. We were unable to resolve the attachments in the smaller specimen.
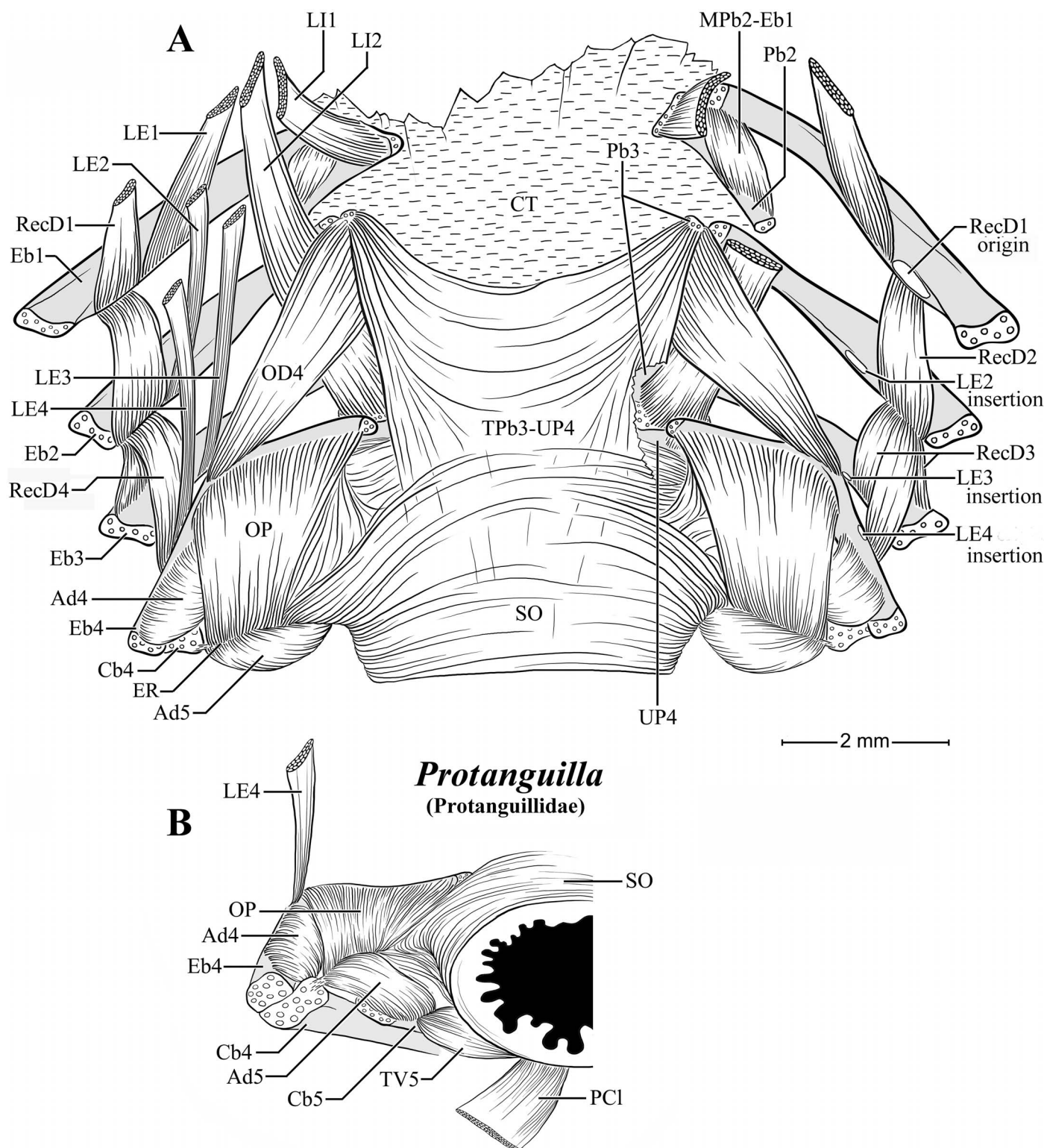
Fig. 2. *Protanguilla palau*, USNM 396051, dorsal (A) and posterior (B) views of gill-arch musculature.

RecD3 originates from both the posterior and anterior edges of Eb3, and inserts together with RecD4 on the posterolateral edge of Eb2 at the origin of RecD2.

RecD4 originates on anterior edge of Eb4, beginning about one-fourth distance from lateral end and extends medially (for insertion see RecD3).

Remarks.—Among elopomorphs, only *Protanguilla* has RecD4.

OP originates broadly on Eb4 dorsoposteriorly medial to attachment of OD4 to Eb4, ventrolaterally joins raphe (ER) with Ad5 dorsoposterolaterally, which then continues medially to SO.

Ad1–3 absent.

Ad4 originates on Eb4 dorsoposterolaterally and inserts ventrally on Cb4 dorsolaterally between the medialmost pair of gill rakers.
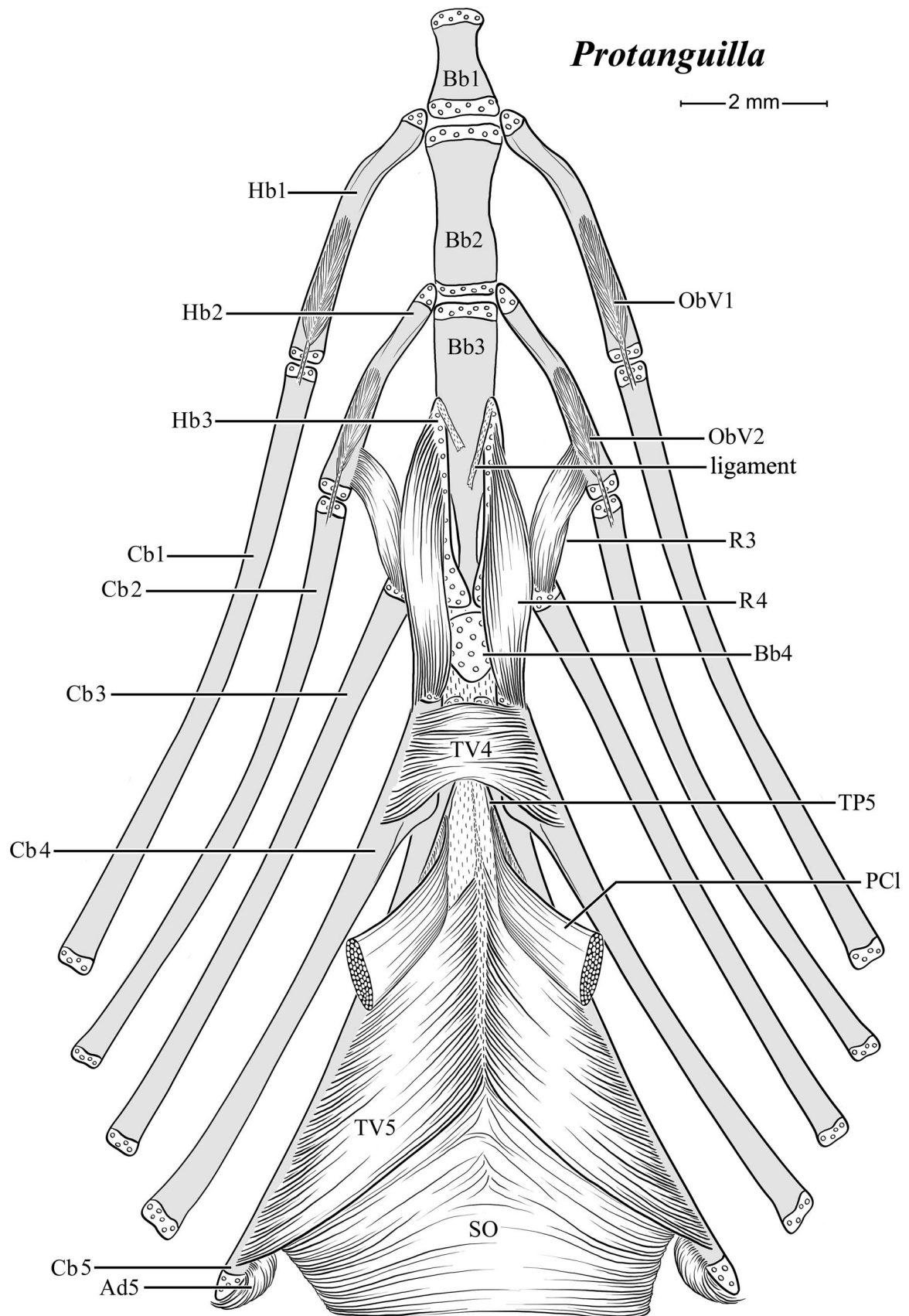
Fig. 3. *Protanguilla palau*, USNM 396051, ventral view of ventral gill-arch musculature.

Ventral gill-arch muscles

Ad5 short, dorsally joins ER with OP, ventrally on Cb5 posterodistally, joining raphe with TV5.

MCb5-TP5 attaches to Cb5 dorso-anteromedially and broadly to associated TP5 posteriorly (not illustrated).

R4Cm absent.

ObV1 originates tendinously on proximalmost ventral surface of Cb1, insertion along distal ventral surface of Hb1.

ObV2 origin tendinous, on ventroproximalmost surface of Cb2, insertion along ventrodistal surface of Hb2.

R1 and R2 absent.

R3 originates on proximalmost ventral surface of Cb3, some fibers mixing there ventrally with R4 muscle fibers; insertion on posterolateral edge of Hb2, not joining ObV2.

R4 originates ventrally on proximalmost surface of Cb4 (just anterior to proximalmost edge of TV4), and inserts along the ventral surface of an elongate cartilaginous Hb3. Muscle fibers mix dorsally with ventroposterior fibers of R3. Additionally, a small dorsal branch of muscle fibers (obscured in Fig. 3) attaches the ventral surface of the proximal cartilaginous end of Cb4 to the ventral surface of the proximal cartilaginous end of Cb3.

Except for *Moringua*, R4 is a relatively small muscle in the eels we studied, but in *Protanguilla* it is well developed and easily mistaken as R4Cm. Its appearance in *Protanguilla* is superficially similar to that of RecCom in *Elops*, but differs in lacking a tendinous attachment to Cb5 and in having a muscular origin on Cb4. It is especially notable that Hb3 is either cartilaginous or absent in eels, but is largely ossified in all other elopomorphs and most other Teleostei. A cartilaginous Hb3 is a synapomorphy of Anguilliformes that was not noted by Johnson et al. (2012).

SPh absent.

TV4 attaches to Cb4s ventroanteriorly, almost meeting (on each side) posterior end of respective R4.

TV5 is V-shaped (apex anterior), attaches broadly on Cb5s posteriorly, and is completely divided in middle by raphe, which joins CT connecting Cb5s anteriorly. TV5 on each side meets posterolateral edge of respective PCl on Cb5. Removal of PCl and freeing CT connecting Cb5 exposes MCb5-TP5 (not illustrated).

PCl originates on the cleithrum ventroanterolaterally and inserts on Cb5 and TP5 anteromedially where it is mostly dorsal to TV4.

Congridae

Conger cinereus Rüppell
Figures 4 and 5

Material.—Dorsal gill-arch muscles, illustrated herein, are from S&J (2004:pl. 21) and descriptions of these muscles (not repeated here) are those contained in S&J (2004:37–38) based on USNM 115969, with the following modification pertaining to MUP4-Eb4, which they described as "on UP4 dorso-posterolaterally, posteriorly becoming broad, thin Ct sheet, which attaches to ventrolateral margin of Eb4 (at angle of Eb4-Cb4 joint) and extends medially, becoming incorporated in SO." We modify this to delete "and extends medially . . . incorporated in SO." Re-analysis indicates MUP4-Eb4 does not become incorporated in SO.

Ventral gill-arch muscles

Description and illustration are based on USNM 311286, ca. 272 mm TL, St. Brandon Rocks (aka Cargados Carajos), Indian Ocean.

R4Cm extends anteriorly from the anteroventromedial surface of Cb4, adjacent to TV4, to the ventromedial surface of Hb2, there meeting the anteromedial attachment of ObV2. It is joined by R4 dorsally at its origin on Cb4.

Nelson (1967a:348) described RC (our R4Cm) in *Conger* as follows, " . . . extends from the proximal end of C4 [our Cb4], with some of its fibers inserting on H3 [our Hb3], others on H2 [our Hb2] in common with O3 [our ObV3]." We assume that the fibers Nelson reported inserting on Hb2 are those we found in common with Obv2. Nelson (1967a:348, 379, and table 1) indicated that ObV3 is present in *Conger* and that R3 is absent. In describing ObV3 in *Conger*, he indicated that "its insertion apparently has been transferred anteriorly [from Hb3] to H[b]2," and that a "rectus (R4) is present only between arches 3–4, extending between the proximal ends of C4 and H3." We initially agreed with Nelson's report, but subsequently found Obv3, which is quite small and is hidden from view by the underlying R4 and R4Cm; we presume that Nelson overlooked R3, as we did initially.

RecCom absent.

ObV1 originates tendinously on the ventromedialmost surface of Cb1 and inserts musculously on the ventromedialmost surface of Hb1.

ObV2 originates tendinously on the ventromedialmost surface of Cb2 and inserts musculously on the ventromedialmost surface of Hb2 (see also R4Cm).

ObV3 is very small, completely excluded in ventral view by the underlying R4Cm; it originates tendinously on the ventromedialmost surface of Cb3 and inserts musculously on Hb3, where it meets R4's anterior attachment (see also R4Cm).

R1 absent.

R2 absent

R3 originates on the ventromedialmost surface of Cb3 and inserts on the ventromedialmost surface of Hb2 (see also R4Cm). Nelson (1967a:349), for *Conger*, indicated that there has been a transfer of the anterior attachment of ObV3 from Hb3 to Hb2 because R3 was absent; however, we found that both ObV3 and R3 are present in our specimen of *Conger*.

R4 (hidden in ventral view by underlying R4Cm) originates on Cb4 anteromedially and inserts on Hb3 ventromedially.

SPh absent.

TV4 attaches to anteromedial edges of the Cb4s and lies just ventral to anteriormost PCl attachments (not illustrated) to Cb5 and TP5.

TV5 attaches laterally on each side to its respective Cb5, there meeting ventromedial attachment of Ad5; it is chevron shaped, lies ventral to the inner, longitudinal SO muscle layer (also see VR) and is divided medially by a raphe.

PCl originates posteriorly on the cleithrum and inserts anteriorly on Cb5 (see also VR below).

Ad5 joins distal end of Cb5 to sub-distal bony end of Cb4 and dorsomedially joins ER.

VR. Nelson (1967a:348–349, fig. 1) described and illustrated the ventral gill-arch muscles of *Conger*. Within his description, he described a ventral retractor. We quote the pertinent parts of his description as follows, "A posterior
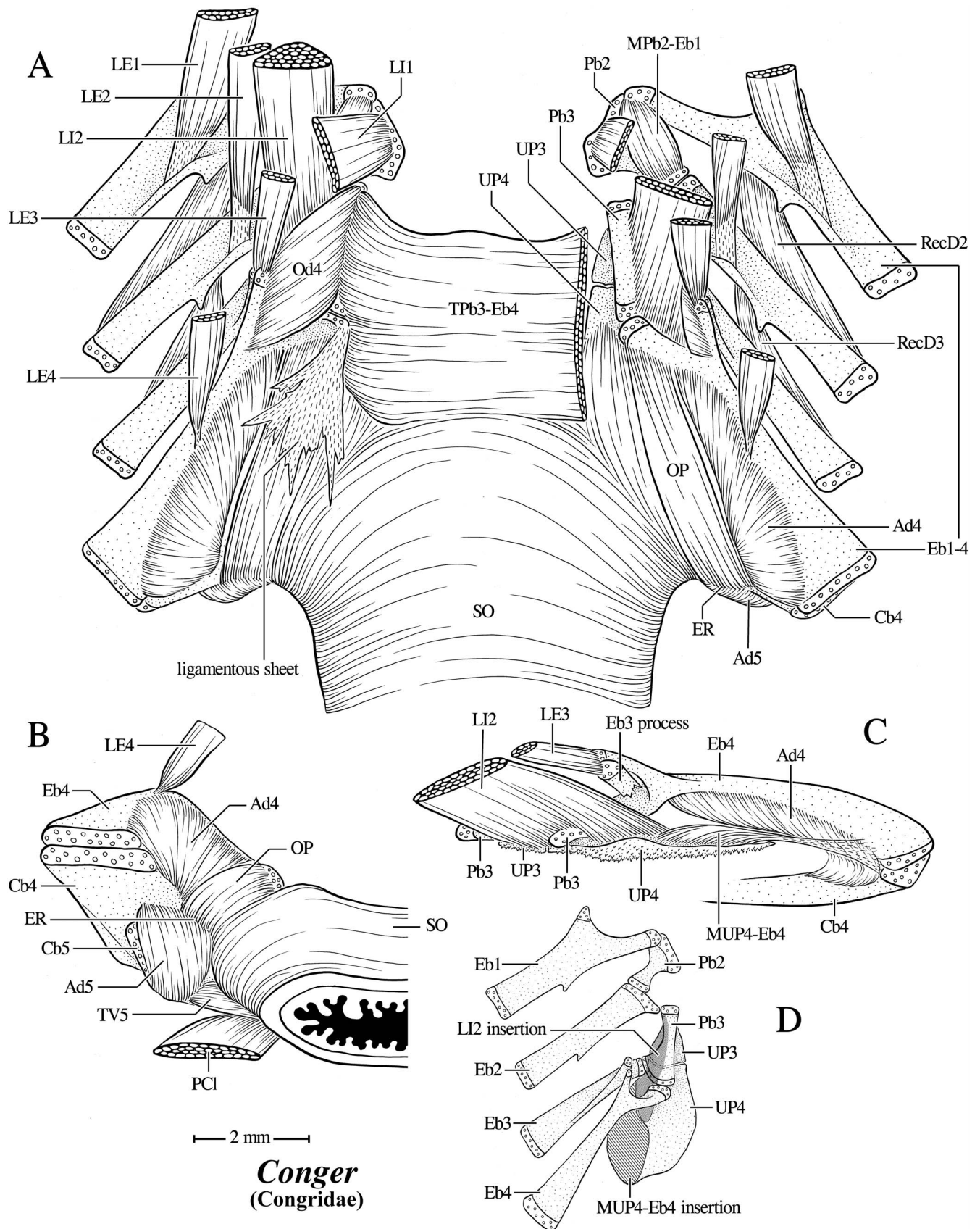
Fig. 4. *Conger cinereus*, USNM 115969, dorsal gill-arch musculature (from S&J:pl. 21). (A) Dorsal view: right-side TPb3-Eb4 and Od4 cut away and ligamentous sheet removed to reveal underlying muscles; (B) left side posterior view; (C) lateral view of right side fourth gill-arch reversed; (D) *C. triporiceps*, ANSP 106182, left-side gill arches with gray areas indicating muscle insertions based on *C. cinereus*.
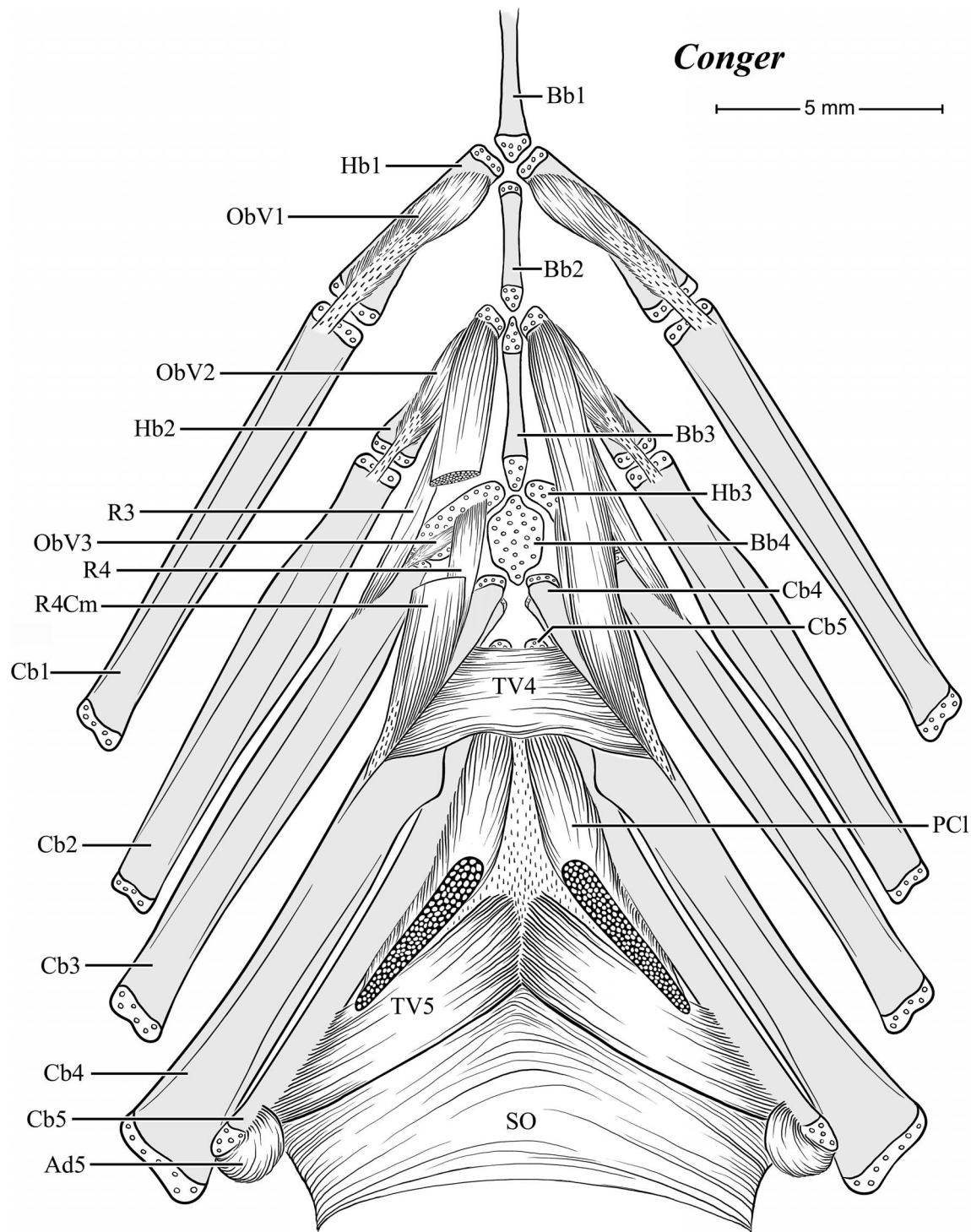
Fig. 5. *Conger cinereus*, USNM 311286, ventral view of ventral gill-arch musculature; right-side R4Cm bisected to reveal overlying R4; Bb1 truncated.

transversus (PT) [our TV5] extends between the distal ends of C5 [our Cb5] of either side . . . A sphincter (S) [our SO] encircles the esophagus and also interconnects C5 of either side. Internal to the sphincter extend longitudinal fibers tending to separate anteriorly, forming a paired muscle, the ventral retractor (VR), attaching to LP [our TP5] and posteriorly extending some distance in the esophageal wall.'' His generalized illustration shows a bisected TV5, dorsal to which a portion of the SO circular layer is removed, thus exposing VR, which he illustrates as a distinct strap of muscle, well separated medially from any other muscle fibers.

Our observation of VR is that it comprises an almost complete sheet of muscle consisting, of a thin, perhaps, single layer of longitudinal fibers, distinct from and internal to an outer circular muscle layer. The muscle fibers of the internal sheet attach on Cb5 along the medial edge of the tooth plate (TP5) associated with Cb5, with only a very shallow separation (divergence) mid-anteriorly in the muscle sheet. We think it a moot point to designate the attachment of the longitudinal muscle layer as a distinct muscle. The longitudinal muscle layer is not shown in our Figure 5; it is completely obscured from view by the ventrally underlying TV5.

Anguillidae

Anguilla rostrata (Lesueur)
Figures 6 and 7

Material.—Dorsal gill-arch muscles are based on USNM 340815, illustrated in Figure 6 (from S&J, 2004:pl. 22); muscle descriptions in S&J (p. 38–39) not repeated here, except to note that GFM1 and GFM2 have been re-interpreted and labeled as Ad1 and Ad2, and that left-side LE4 in their description and figure 22 is erroneously indicated as extending anteriorly medial to, rather than lateral to LI1. Although not noted by S&J (2004:39), dorsal gill-arch muscle RecD3 originates slightly ventral to the anterior edge of Eb3 and inserts on a well-defined bony process on the posterodorsal margin of Cb2 just lateral to mid-length.

Ventral gill-arch muscles

Described and illustrated here based mostly on USNM 190998, 320 mm specimen, with additions (for damaged muscles) from USNM 314441, 296 mm specimen.

R4Cm originates on the ventromedial surface of Cb4 adjacent to TV4 and extends anteriorly to the posterodistal edge of Hb1, where it attaches jointly and tendinously with the anteromedial end of R2. R4Cm passes ventral to R4, R3, ObV3, and ObV2, and variously shares a few fibers (not illustrated) with some of these muscles. Additionally, only unilaterally, there may be independent fibers (not illustrated) in the area dorsal to R4Cm that attach Hb3 to Hb2.

Nelson (1967a) did not specify the attachments of R4Cm (his RC) in *Anguilla,* but stated that the muscles of *Anguilla* are ''rather similar'' to those of *Conger.* In general, we agree, but R4Cm in *Conger* inserts anteriorly on Hb2, whereas it inserts on Hb1 in *Anguilla.* In Nelson's (1967a:348) discussion of *Conger*, he stated that R4Cm (his RC) extends from Cb4 (his C4) with some of its fibers inserting on Hb3 (his H3) and others on Hb2 (his H2) in common with those of ObV3 (his O3), implying that the anteriormost insertion of R4Cm is on Hb2. This implication is confirmed in his illustration (Nelson, 1967a:fig. 1) of the ventral muscles of *Conger.*

RecCom absent.

ObV1 distinct, extends tendinously from ventromedial-most surface of Cb1 to mid-ventral surface of Hb1.

ObV2 extends from ventromedialmost surface of Cb2 to ventromedialmost surface of Hb2.

ObV3 small, short, weakly developed, easily overlooked or destroyed in dissection, extends from ventromedialmost end of Cb3 to Hb3; ObV3 is completely obscured ventrally by both R4 and R4Cm (see insert, upper left, of Fig. 7).

R2 short, very broad, extends from ventroanteromedial-most surface of Cb2 to posterior edge of Hb1-Cb1 joint, where it meets R4Cm.

R3 extends from ventroanteromedialmost surface of Cb3 to Hb2 ventroposteriorly.

R4 extends from Cb4 ventroanteromedially to Hb3 ventrally; muscle fibers mix ventrally with those of R4Cm.

SPh absent.

TV4 attaches to the anteroventromedialmost surface of Cb4s, there meeting posteromedialmost edge of R4Cm, and underlies medialmost end of PCl on Cb5 and TP5.

TV5 attaches laterally on each side to its respective Cb5, there meeting the ventromedial attachment of Ad5; it is chevron shaped, with a median raphe, and is only weakly demarcated posteriorly from SO. See also VR in *Conger.*

Ad5 arises dorsally from ER with lateral tendinous attachment to Cb4 posterodistal end; ventrally on postero-distal half of Cb5.

PCl inserts broadly on ventroposterior surfaces of Cb5 and TP5 anteriorly dorsal to TV4; origin on cleithrum not determined.

Remarks.—Nelson (1966a:394) reported that Bb3 is absent in *Anguilla.* It is also absent in our 228 mm specimen but is a moderately developed, slender cartilaginous rod in our 328 mm specimen, and probably represented as two tiny linearly separated cartilages in the other two specimens.

Synaphobranchidae

Synaphobranchus kaupii Johnson
Figures 8–10

Material.—Dorsal gill-arch muscles are based on *Synapho-branchus* sp., USNM 316662, illustrated in Figure 8 (from S&J, 2004:pl. 23); muscle descriptions in S&J (p. 39) not repeated here. We note that ER is present, but is not visible in any of their illustrated views.

Ventral gill-arch muscles

Ventral gill-arch muscles (Figs. 9, 10) described and illustrated from *S. kaupii* Johnson, ca. 360 mm TL, USNM 396609.

SPh, viewed dorsally, originates broadly on Cb4 and attaches anteriorly first on medial end of Cb3 dorsal to anterior attachment of R4; a second portion of SPh appears to originate on Cb3 and associated TP3 and extends anteriorly and fuses with the anteromedial edge of the first portion; the two portions continue anteriorly and are joined by muscle fibers from Hb2 and Hb1, ultimately attaching to Hyh and AntCh. SPh in dorsal view obscures R4Cm, R4, and R3, all three of which appear to fuse dorsally with SPh (and each other). Viewed ventrally, the contributions to SPh and extent of R4Cm, R4, and R3 are partially obvious. As suggested by Nelson (1967a:362), ontogenetic studies may clarify the composition and nature of SPh.

R1 and R2 apparently absent.

R3 and R4, see SPh.

R4Cm, see SPh.

RecCom absent.

ObV1 originates tendinously on ventromedialmost sur-face of Cb1 and attaches musculously on ventrolateral surface of Hb1.

ObV2 originates tendinously on ventromedialmost sur-face of Cb2 and attaches musculously on ventrolateral surface of Hb2.

ObV3 absent.

Ad5 absent. S&J (p. 72) erroneously indicated that Cb5 was absent in *Synaphobranchus*; Ad5 should have been so indicated.

TV4 attaches broadly on ventromedial surface of each Cb4, ventral to origin of PCl on Cb5s.

TV5 attaches anteriorly on Cb5 near closely associated posteriormost TP on each side (of group of four TPs on each side) and extends broadly posteriorly; more-or-less
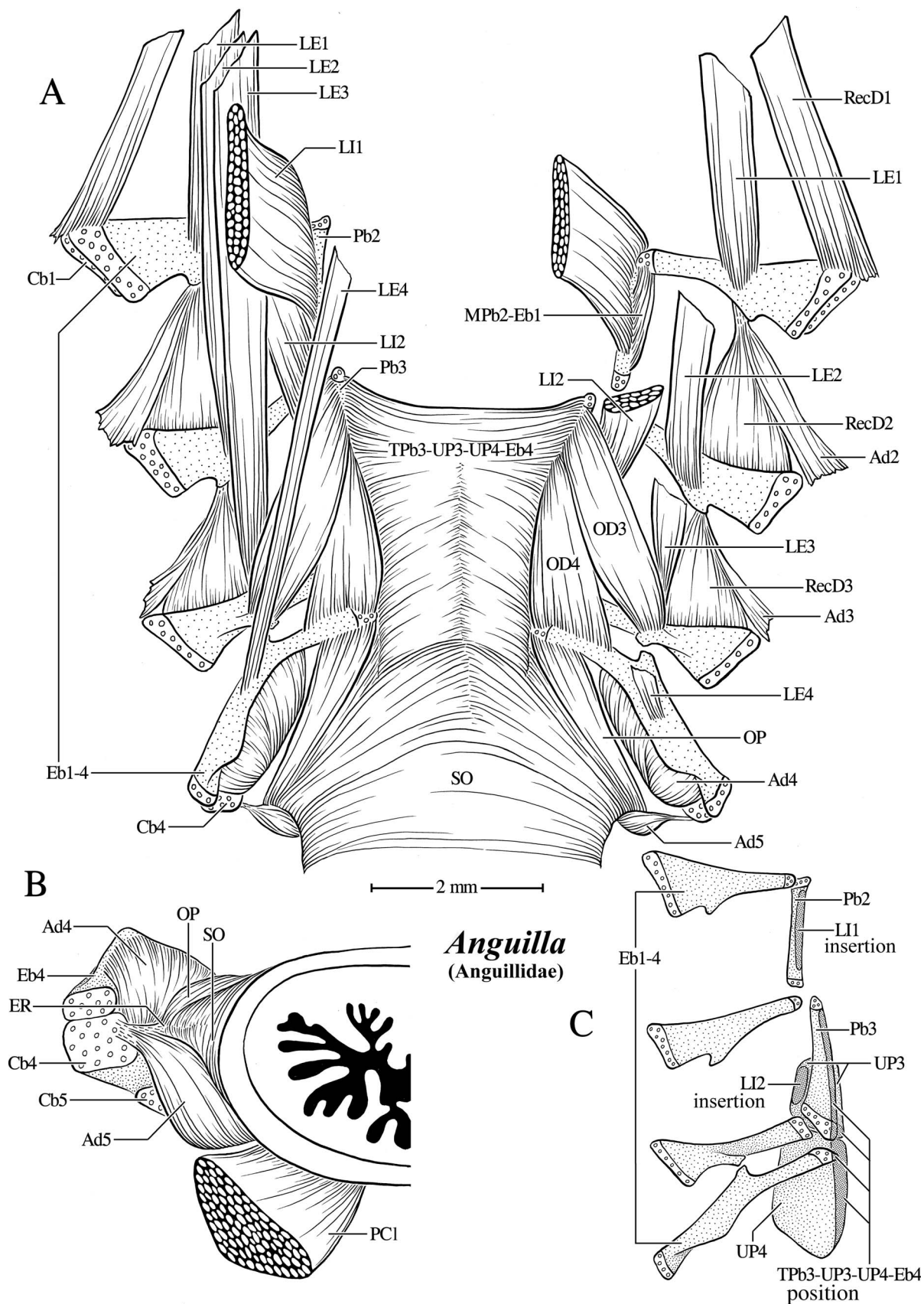
Fig. 6. *Anguilla rostrata*, USNM 340815, dorsal gill-arch musculature (from S&J:pl. 22; with labels GF1 and GF2 re-interpreted and re-labeled as Ad1 and Ad2). (A) Dorsal view (left side LE4 should pass lateral to LI1; right-side LI1 deflected medially to reveal MPb2-Eb1, some levators truncated); (B) left side, posterior view; (C) left-side dorsal gill-arch skeleton with shaded areas to show muscle insertion positions.
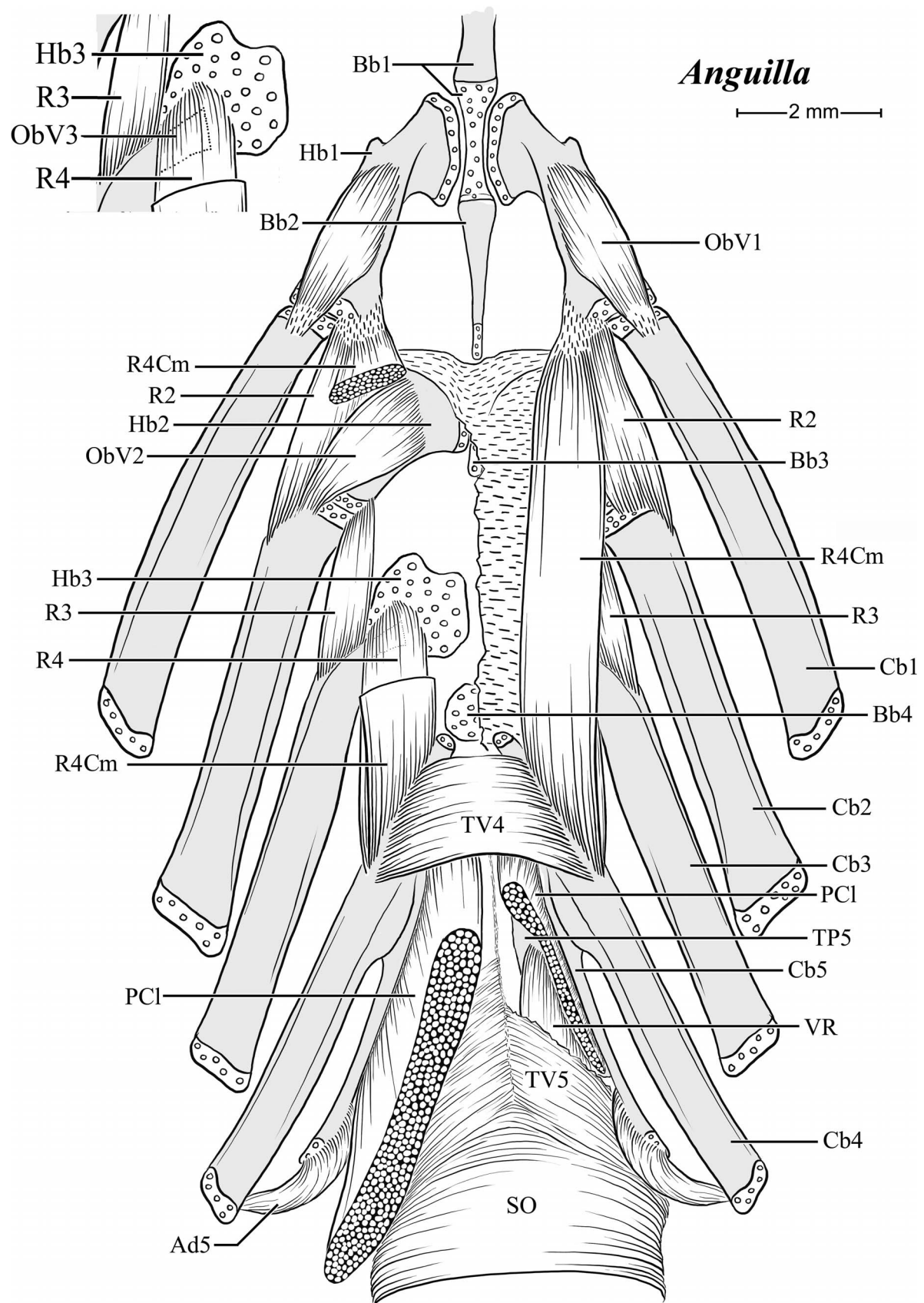
Fig. 7. *Anguilla rostrata*, USNM 190998 (with additions for damaged muscles) from USNM 314441, ventral view of ventral gill-arch muscles; right-side R4Cm bisected to reveal overlying muscles; Bb1 truncated; enlarged small inset drawing at upper left, to show position of ObV3 (broken lines) dorsal to R4.
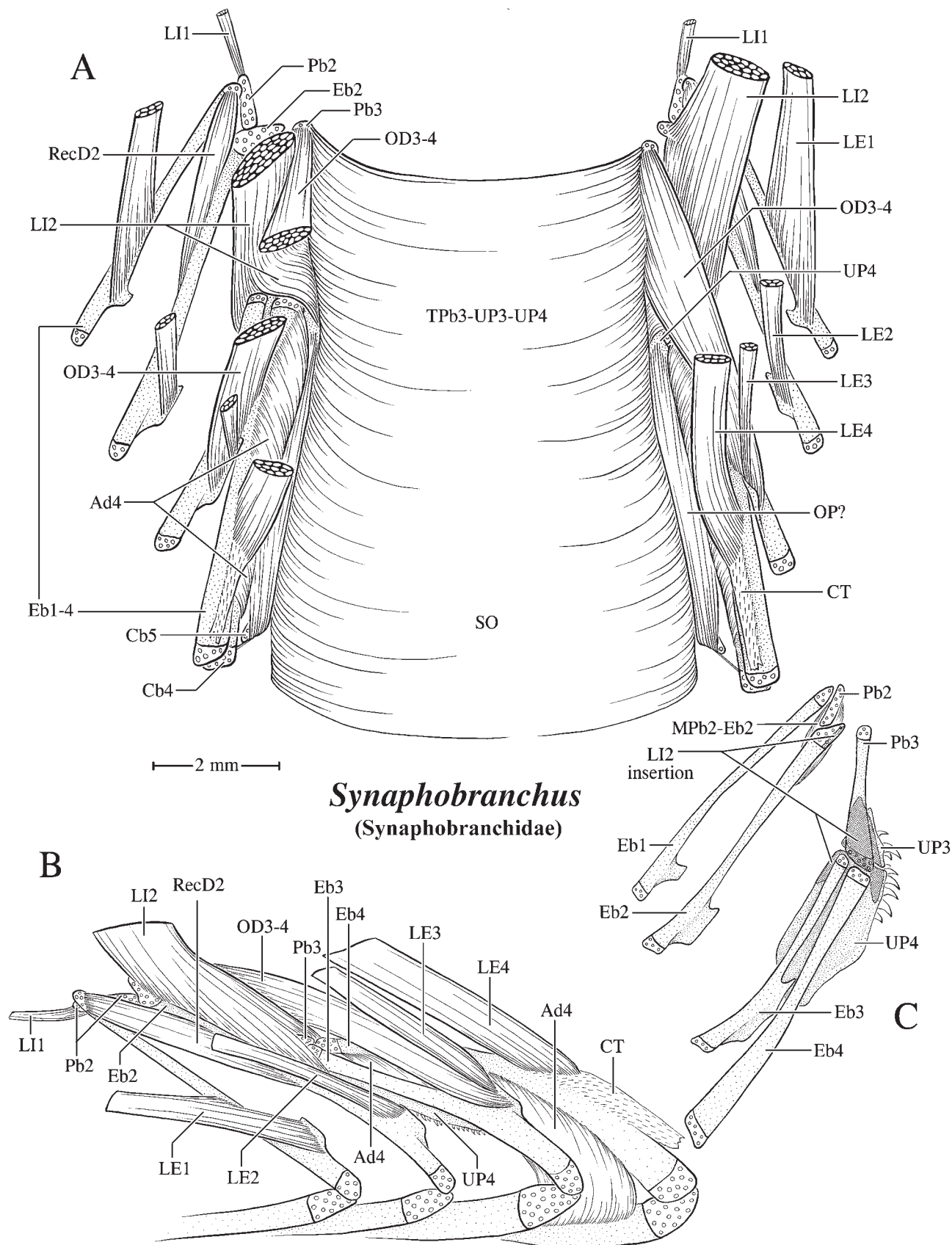
Fig. 8. *Synaphobranchus* sp., USNM 316662, dorsal gill-arch musculature (from S&J:pl. 23); ER present, but not shown in any view. (A) Dorsal view: left-side OD3-4 bisected to expose underlying muscles, MPb2-Eb2 not shown (see C); (B) lateral view, right side reversed, SO not shown; (C) *S. kaupii*, VIMS uncataloged, cleared-and-stained, left-side dorsal gill-arch skeletons, with MPb2Eb2 and insertion position of LI2 from USNM 316662 indicated.
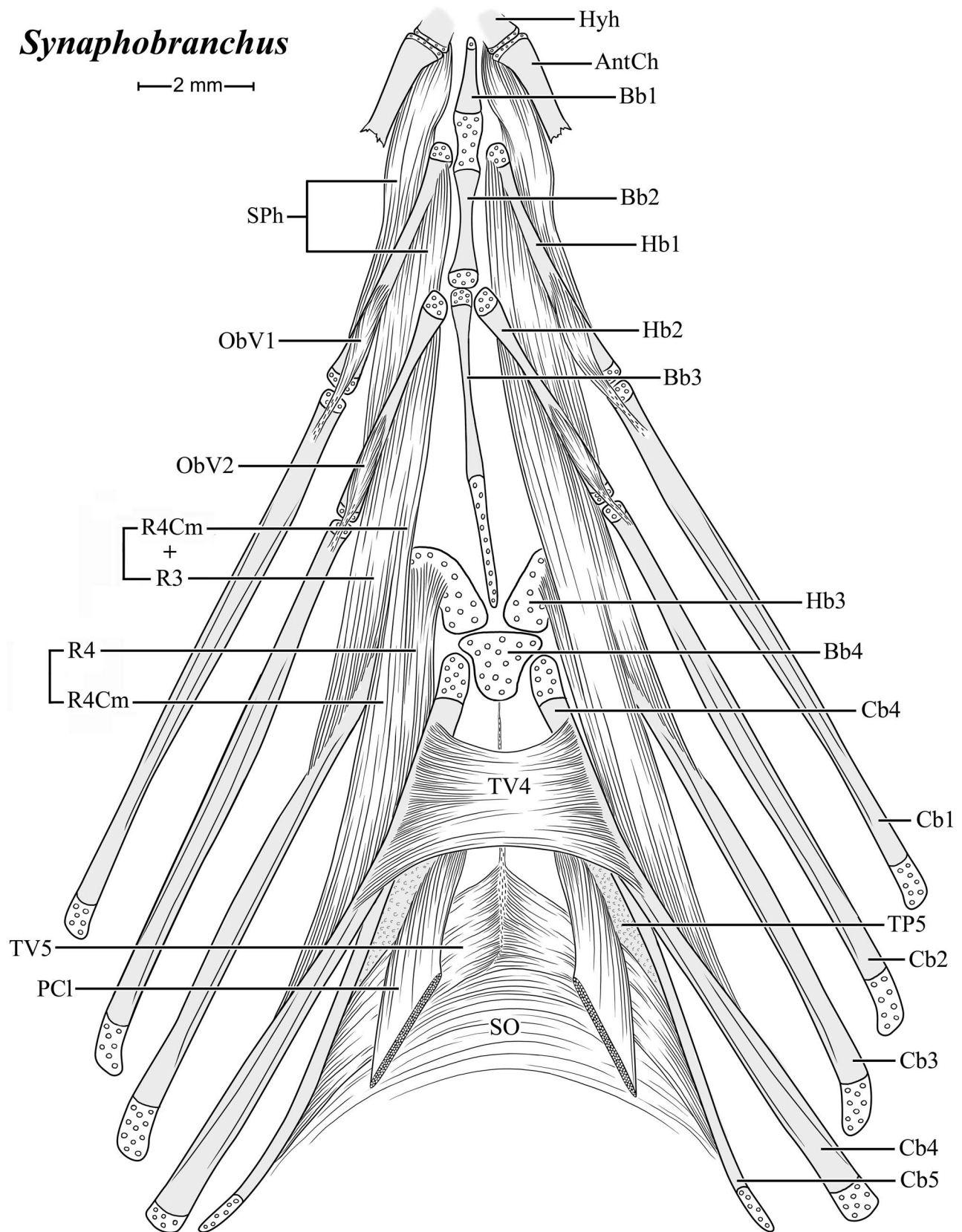
Fig. 9. *Synaphobranchus kaupii*, USNM 396609, ventral view of ventral gill-arch muscles; AntCh and Hyh truncated.

continuous posteriorly with SO, but distinct anteriorly, as indicated by presence of a median raphe, which continues finely anteriorly and is attached to Bb4.

PCl originates on cleithrum and inserts along the posteromedial edges of TP5 and Cb5.

***Simenchelys parasitica* Gill**
Figures 11–13

Material.—USNM 372009, ca. 339 mm TL, Taiwan; 031727, ca. 325 mm, off Massachusetts.
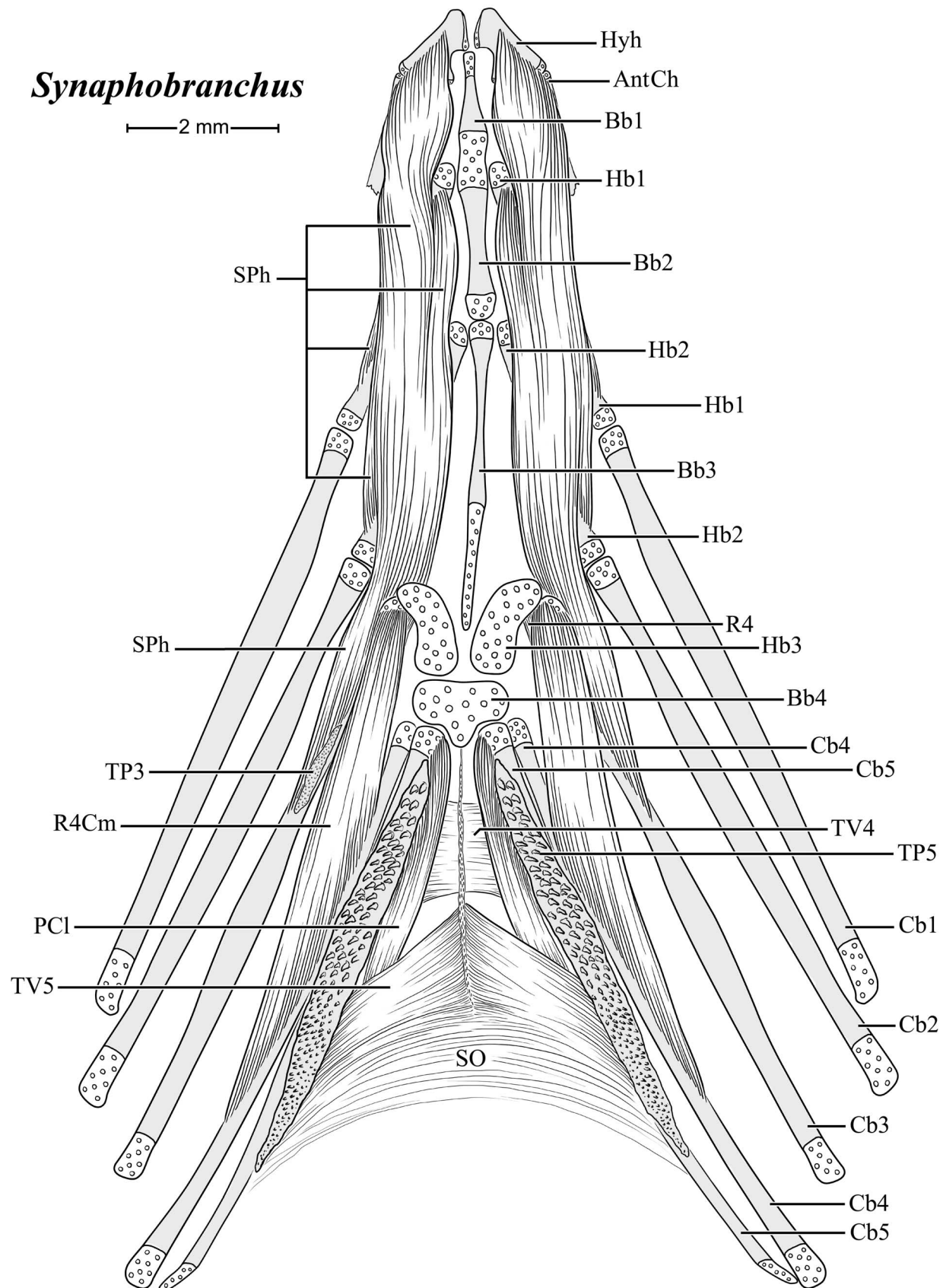
Fig. 10. *Synaphobranchus kaupii*, USNM 396609, dorsal view of ventral gill-arch muscles; AntCh truncated.

Dorsal gill-arch muscles

Remarks.—Most muscles heavily invested with fine fascia; all levators inclined almost horizontally for much of their length.

LE1 inserts broadly, laterally on dorsoposterior margin of Eb1; anterior muscle surface tightly bound to CT of orobranchial chamber roof.

LE2 inserts broadly, laterally on dorsoposterior margin of Eb2.

LE3 inserts narrowly tendinously on dorsoposterolateral-most edge of Eb3 and strongly tendinously on Eb4 mid-anterolaterally, meeting (almost joining) anterodistal edge of OD4 on Eb4.

LE4 inserts on Eb4 beginning about mid-dorsoposteriorly and extending almost to lateral end of bone, meeting Ad4 dorsally.

LI1 short, inserts on Pb2 anterolaterally.

LI2 inserts broadly on dorsoposterior surface of Pb3, extending onto posteromedialmost edge of Eb3; dorsomedialmost surface lies ventral to OD4.

TPb3 connects Pb3s dorsally, meeting medial edge of OD4; separation from SO indicated by slight notch on each side of posterior margin of TPb3.

MPb2-Eb1 short, attaches to Pb2 dorsally and Eb1 dorsomedially.

OD3 absent.

OD4 anteriorly on dorsomedial surface of Pb3, meeting anterolateral edge of TPb3; posteriorly on Eb4 mid-dorsally, there meeting LE3 ventroposteriorly.

OP originates dorsally on Eb4 dorsomedially and adjacent surface of UP4, meets ER ventrally, and attaches on tendon that joins Cb4 posterolaterally with dorsolateral end of Ad5.

DR (not illustrated) originates anteriorly on dorsolateral surface of UP4 and ventromedialmost surface of Eb4 and extends posteriorly as continuation of SO inner (longitudinal) muscle layer.

Nelson (1967a) first reported and described this muscle, which he found in all the eel taxa he examined, and which he termed "retractor dorsalis" (not equivalent to Rosen's [1973] retractor dorsalis, which originates on anterior vertebrae). Nelson, however, did not report that fibers of the muscle might also attach to Eb4. S&J (2004:39) reported that, depending on taxon, the muscle fibers attaching to UP4 variously continue onto Eb4 (*Conger, Synaphobranchus*) or Pb3, UP3, UP4, Eb4 (*Anguilla*), and although these fibers are also continuous with the longitudinal SO muscle layer, their configuration varies depending on the taxon. In *Synapho-branchus*, S&J tentatively termed the muscle OP, "strap of muscle attaching dorsally to posteromedial surface of UP4 and ending ventrally at ER [not illustrated], which is at level of Cb4, and extends laterally as slender tendon to poster-odistal end of Cb5; inseparable medially, and ventral to ER from SO," which condition they did not illustrate. The muscle fibers attaching to UP4 on each side of the gill arches in *Synaphobranchus* form a short separate branch of OP. See also remarks following VR.

Ad1, Ad2, Ad3 fan-shaped, each spanning the anterior surface of the joint formed by its respective Eb and Cb.

Ad4 originates dorsally, broadly on Eb4, there meeting LE4 and inserts ventrally on Cb4 dorsally, beginning laterally at inner axil of Eb4-Cb4 joint and extending broadly medially (attachment not illustrated).

Ventral gill-arch muscles

R4Cm long, extends anteriorly from Cb4 anterior process, where it meets anterolateral edge of TV4, passes ventral to R4 origin on Cb4 and then fuses with R3 as both attach along posterior edge of Hb2. A few muscle strands continue anteriorly past Hb2 to join SPh.

It was possible to strip R4Cm and R3 from the ventral surface of SPh, but the separation of the muscles appears to be artificial.

RecCom absent.

R1 and R2 apparently absent.

R3 and R4 present (see R4Cm above).

ObV1, 2, 3 absent.

Absence of ObVs is possibly associated with the extremely well-developed ventral gill-arch musculature. The closely related *Synaphobranchus*, in which the musculature is much more moderately developed, possesses ObV1 and Obv2.

TV4 (see R4Cm above) attaches on anteromedial edge of Cb4s.

TV5 divided medianly by raphe, attaches along posterior edge of each Cb5 posteriorly and is continuous posteriorly with SO. The posterior margin of TV5 is slightly thicker than the adjacent SO muscle, which has a weak continuation of the median raphe of TV5.

PCl long, originates on cleithrum and inserts anteriorly on Cb5 anteromedially.

SPh largest and most complex gill-arch muscle, located dorsal to ventral gill-arch muscles. In dorsal view, a few muscle strands attach to anteromedialmost edge of left-side Cb5 (no such attachment on right-side); attaches on most of dorsomedial surface of Cb4, then extends anteriorly and attaches to Cb3 and Cb2 anteromedially, Cb1 posterome-dially, and lateral sides of Bb4, Bb3, and Bb2 and almost completely covers Hb3, Hb2, and Hb1; ends anteriorly with attachment (not shown) to AntCh and Hyhs anterome-dially. SPh, muscle fibers become sparse between Cb4 and Cb3. This muscle is much enlarged compared with that of *Synaphobranchus* and differs from *Synaphobranchus* in attach-ing to Bb2 and much reduced Bb3 and Bb4.

Our removal of the gill arches was completed before we recorded the anteriormost attachment of SPh. Jaquet (1920:50–51, and pl. 3:80b) described and illustrated this muscle (his hyoidéo-branchiale), on which we relied for our description of its anterior attachment, but he did not illustrate or specify that SPh attached to the ceratohyals, which we assumed, based on *Synaphobranchus*. His de-scription and figure of the other muscles and their attach-ments are more generalized than ours.

Nelson (1967a) did not specify the anterior attachment of SPh (his SP) in any of the taxa for which he indicated its presence. As for the other attachments, his illustration of SPh in *Moringua* (1967a:fig. 5) appears to indicate attach-ments to Cb4, 3, 2, Hb3, 2, 1, Bb3, 2, and possibly, slightly, to Cb1. His illustration of SPh in *Kaupichthys* (Nelson, 1967a:fig. 7) appears to indicate attachments to Cb3, 2, 1, Hb1, 2 (Hb3 and Bb3, 2 are absent). He did not illustrate SPh in the muraenid *Uropterygius*, but indicated that its ventral muscles were similar to those of *Kaupichthys*, For *Gymnothorax*, also a muraenid, he illustrated (Nelson, 1967a:fig. 10) a highly subdivided SPh, of which only the subdivisions are labeled (abbreviations are those of Nel-son): attractores intermediales (IA1–2), attractores laterales (LA1–4), attractores mediales (MA1–3), attractores obliqui
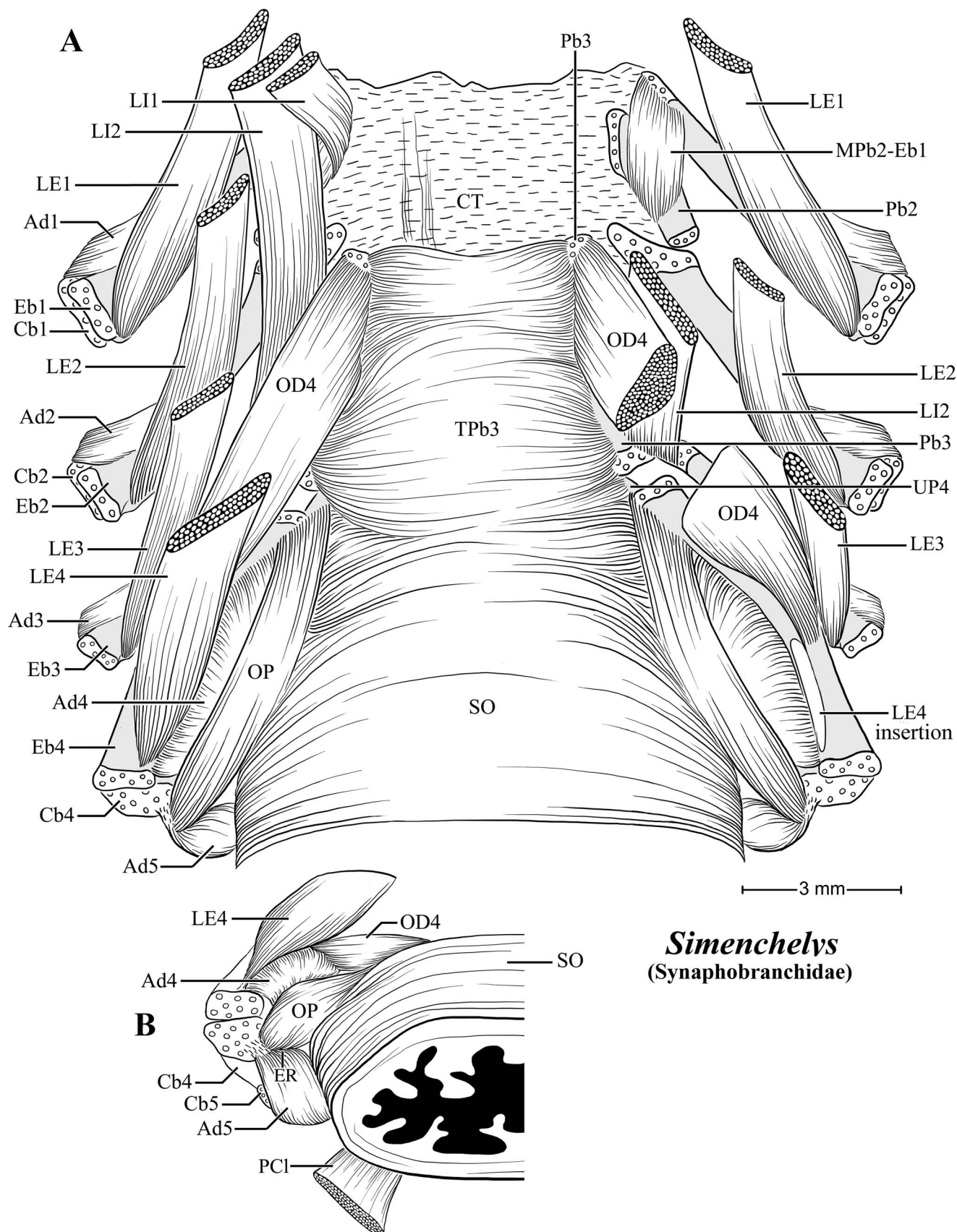
Fig. 11. *Simenchelys parasitica*, USNM 372009; (A) dorsal view of dorsal gill-arch muscles; right-side OD4 bisected to show insertion of LI2 and unilateral attachment of TPb4 to UP4; (B) left side, posterior view.
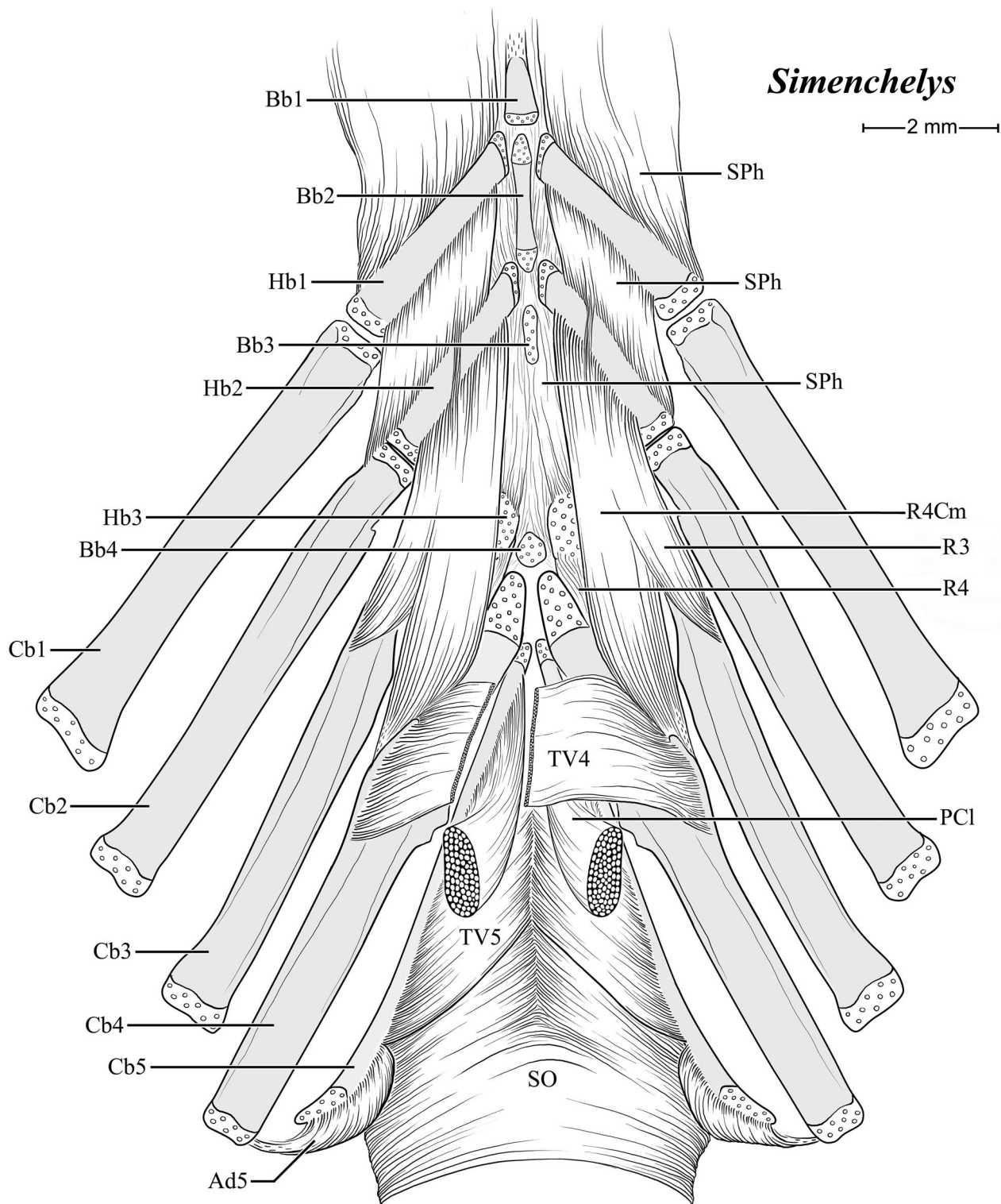
Fig. 12. *Simenchelys parasitica*, USNM 372009; ventral view of ventral gill-arch muscles; TV4 bisected to expose insertion of PCl; SPh truncated.

(OA1–2), and sphincters branchiales (SR 1–4). SR1–4 each branches off a lateral attractor LA1-4, loops around an associated gill opening, and attaches in order to Cb 4, 3, 2, 1; LA4, 3, 2, originate, in order, on Cb4, 3, 2, and attach, in order, on Cb3, 2, 1; LA1 also attaches on Cb1, but its anterior attachment is not indicated. MA1–3 originate together on TP5, and one, each, attaches to Cb3, Cb2, and Cb1. The posterior attachments of OA1 and OA2 originate broadly on Cb1 and Cb2, respectively, but their anterior-most attachments are not indicated. IA1, IA2A, IA2B originate on Cb4 and extend anteriorly, variously attaching to Cb3, 2, 1, but their anteriormost attachments are not indicated. With so many SPh branches with non-indicated anterior attachments, all (or many) extensions of the branches either combine before attaching to the hyoid apparatus, or there are several separate attachments along the hyoid apparatus.

Ad5 dorsolaterally joins ER and tendon with OP, and ventromedially joins Cb5 posterolaterally.

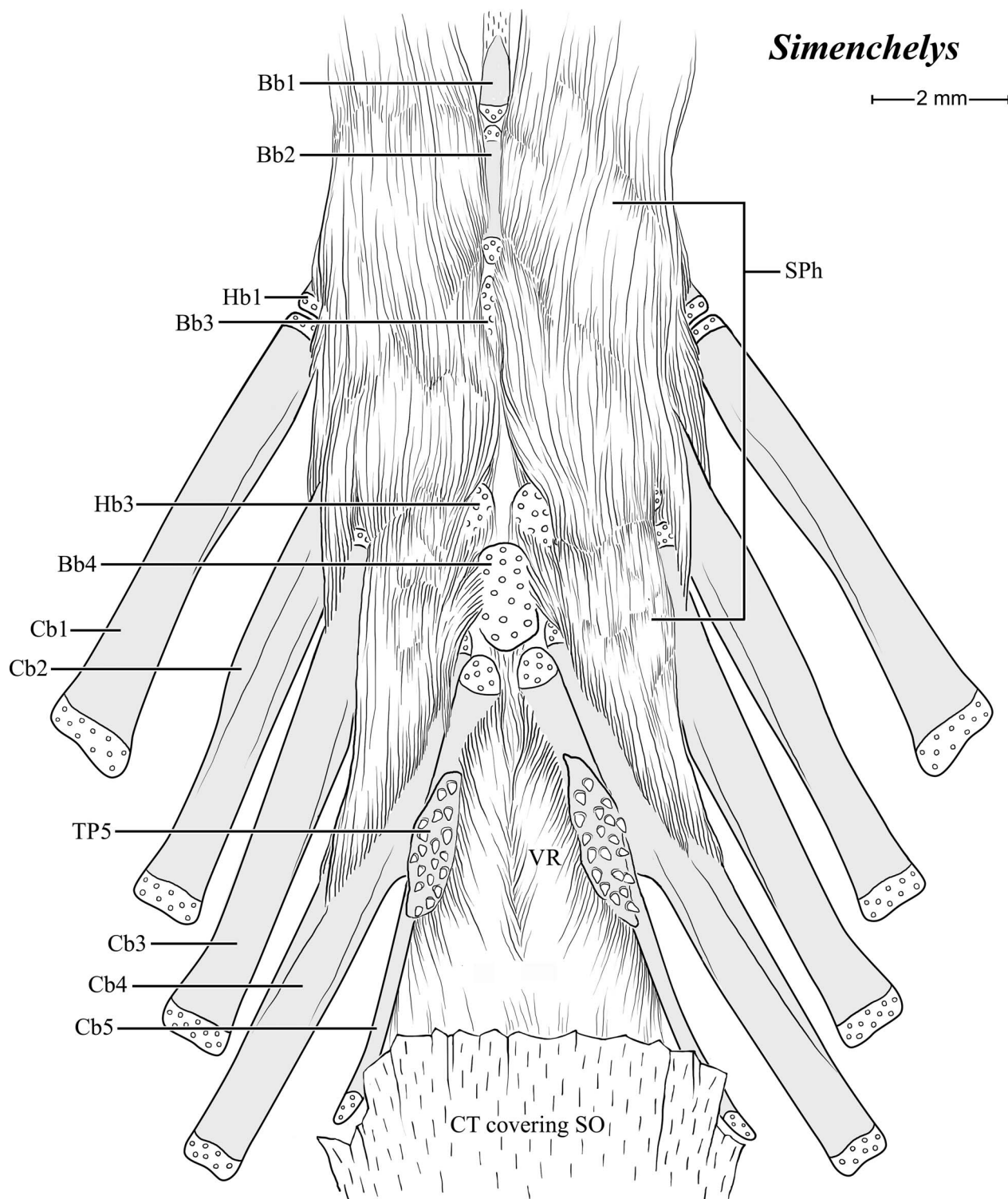VR attaches broadly along Cb5s and TP5s.

Fig. 13. *Simenchelys parasitica*, USNM 372009; dorsal view of ventral gill-arch muscles; SPh truncated.

Serrivomeridae

Serrivomer beanii Gill and Ryder

Remarks.—Gill-arch muscles not illustrated, nor described previously. Tighe (1989) described and illustrated many aspects of the osteology and external features of *Serrivomer*, but not the muscles. We further note for the first time that the epibranchials of *Serrivomer* completely lack gill filaments, a condition we have not seen elsewhere. We assume the absence is associated with the additionally unusual condition that the epibranchials are excluded from the branchial chamber by a continuous sheet of black tissue that completely sheathes them. The black tissue is a non-muscular dorsoanterior extension of the sphincter oesophagi that extends anteriorly along the entire anterior surface of the cleithrum, thence completely along the dorsal surface of the branchial chamber, from which tissue extends posteroventrally, completely attaching along the posteromedial edge of the fourth arch, the dorsolateral surfaces of

the third and second arches, and much of the dorsal surface of ceratobranchial 1. From that point the tissue continues anteriorly into the oral chamber.

Material.—*Serrivomer beanii,* USNM 315418, three specimens, ca. 260 mm TL, ca. 365 mm TL, and ca. 545 mm + missing significant portion of posterior body, Atlantic, 32°09′N, 64°11′W; USNM 383143, ca. 590 mm TL, Atlantic, ca. 40°N, 67°30′W. The gill-arch muscles are complex and fragile. All specimens were damaged variously during dissection, and the description is based on a composite of what could be discerned from them.

Dorsal gill-arch muscles

TD (further study required; see also Remarks above following *Serrivomer beanii*). Dorsally, there is a thin sheet of whitish muscle that originates as an extension of the dorsal transverse, or circular, esophageal muscle layer. It first, and apparently only, attaches on each side to the posterodistal cartilaginous surface of each Cb4 and extends anteriorly, gradually tapering anteromedially without attaching to any other gill-arch element. Ventral to the circular layer, is the longitudinal esophageal muscle layer that extends anteriorly and somewhat laterally and attaches on the medial surface of each Pb3 (TPb3). Separate, more posterior strands of the longitudinal muscle layer attach to UP4 (TUP4). These muscle layers overlie the thin, black nonmuscular tissue layer that lines the pharyngeal cavity.

LE1 broad, but inserts finely on medialmost tip of Eb1 together with the anterior end of RecD2.

LE2 slender, inserts on Eb2 well medial to tripartite joint formed by distal end of Eb2 with posterior end of Pb2 and anterior end of Pb3.

LE3 inserts on cartilaginous tip of Eb3 levator process, which joins bony process on Eb4.

LE4 inserts on Eb4 dorsally just lateral to mid-length.

LE4 prime (needs verification), less developed than LE4, inserts on anteroventral edge of Eb4 close to lateral edge of UP4.

LI1 inserts broadly along rod-like portion of Pb2.

LI2 inserts on dorsal surface of tripartite joint formed by medial cartilaginous tips of Eb3 and Eb4 and posterior cartilaginous tip of Pb3.

MPb2-Eb1 extends from the anteromedial corner of the fan-like medial end of Pb2 to the medialmost tip of Eb1.

OD apparently absent (see Ad4).

Ad1–3 absent.

Ad4 originates broadly on Eb4 dorsally and inserts ventrally on Cb4 posterolaterally.

OP absent

RecD1 absent.

RecD2 absent.

RecD3 joins distal cartilaginous tip of Eb3 to distal cartilaginous tip of Eb2.

RecD4 absent.

Ventral gill-arch muscles

MCb4-Cb5-TP5 (musculus ceratobranchialis 4-ceratobranchialis 5-laminalis dentalis 5), tiny, originates on distalmost bony surface Cb4 and inserts on distal bony surface of Cb5 and associated TP5 (possibly unique to *Serrivomer*).

R4Cm originates finely tendinously with musculous origin of R4 on Cb4 just lateral to TV4, and extends anteriorly to ventral surface of joint between Cb1 and Hb1.

RecCom absent.

ObV1, 2, 3 very tiny muscles, easily destroyed; each originates on distalmost ventral surface of its respective Cb and inserts on the proximalmost ventral surface of its respective Hb. ObV3 hidden from view by ventrally underlying R4.

R1 originates finely on Cb1 close to Cb1-Hb1 joint and Obv1, extends freely far anteriorly until meeting opposite R1 at and attaching to anterior tip of Bb1, thence separating again and extending much further anteriorly and attaching to anteromedial surface of anterior ceratohyal.

R2 originates finely on Cb2 close to Cb2-Hb2 joint and inserts broadly on Hb1.

R3 originates on proximalmost ventral surface of Cb3, some fibers mixing there ventrally with R4 muscle fibers; insertion on posterolateral edge of Hb2, not joining ObV2.

R4 originates on bony ventral flange near medial end of Cb4 and inserts along the posteroventral surface of Hb3.

SPh absent.

MHb1-ChA (musculus hypobranchialis 1-ceratohyal anterioris) extends anteriorly from ventrodistalmost surface of Hb1 and attaches to anterior end of anterior ceratohyal. Possibly only present in *Serrivomer*.

MCb3-Hb1 (musculus ceratobranchialis 3-hypobranchialis 1), extends from ventrodistalmost end of Cb3 to Hb1. Possibly only present in *Serrivomer*.

PCl originates on the cleithrum as a broad sheet-like anterior extension of the hypaxial musculature, becoming condensed and rodlike anteriorly as it extends dorsally and inserts on Cb5 and Cb4.

TV4 attaches to Cb4s ventroanteriorly, almost meeting (on each side) posterior end of respective R4.

TV5 questionably absent.

Ad5 small, connects bony surface of Cb4, just proximal to cartilaginous posterior tip, to distal cartilaginous tip of Cb5.

Serrivomerid interrelationships

Tighe (1989:615) briefly recounted the classsificatory history of the Serrivomeridae and noted errors and variations in past systematic treatments of the family. He concluded that the interfamilial relationships of the Serrivomeridae were still unresolved. As noted by Tighe, Regan (1912) first assigned *Serrivomer* to a family, the Nemichthyidae. Among the earlier publications, Nelson (1966a:402) noted the similarity of the gill arches of *Serrivomer* to those of *Anguilla*, but recognized a group Serrivomeridae and Nemichthyidae within a larger Anguilloidei stating, "The consensus seems to favor the view that the group is a natural one." Although he followed this remark by stating the "gill arch structure may be consistent with the opinion that [the Serrivomeridae and Nemichthyidae] are closely related, but can neither confirm nor refute this opinion. In any event, the Nemichthyidae is here included in the anguilloid lineage for want of clear evidence to the contrary." We mention this history as it has some relevance to reports in molecular studies of anguilliform interrelationships.

Molecular studies are the most recent publications dealing with the interrelationships of Serrivomeridae (Se), Anguillidae (An), and Nemichthyidae (Ne). In the following, we summarize what these studies report regarding the interrelationships of the three families, simplifying the numer-

ous branchings within the overall cladograms to stress the monophyletic clades or lack thereof, of the three families An, Se, Ne. An additional abbreviation (X) is included to represent one or more of the four saccopharyngiform families, which intrude on these interelationships.

1. Obermiller and Pfeiler (2003), 11 eel families, two mitochondrial genes, two trees. Many sub-branches including other eel families are present separating (An+Ne) from (Se) in each of the anguilliform portion of the two trees:
    a) Single most parsimonious tree includes a monophyletic (An+Ne) in the third main branch up from the basal root of the anguilliform portion of the tree, and (Se) in the sixth main branch up the tree.
    b) Neighbor-joining tree includes a monophyletic (An+Ne) in the fifth main branch up from the basal root of the anguilliform portion of the tree, and (Se) in the sixth branch up the tree.
2. Inoue et al. (2010), 19 eel families, 36 mitochondrial genes, best scoring maximum likelihood tree:
    a) (An) is sister group of (Ne+Se).
3. Johnson et al. (2012), 20 eel families, four best scoring maximum likelihood trees:
    a) whole mitochondrial genome, $12_{n_r}3_rRT_n$ data set (13,056 bp): (Ne) sister group of (An+Se)
    b) $12_{n_r}RT_n$ data set (10,028 bp): (Ne) sister group of (An+Se)
    c) $12_{n_r}3_rRT_n$ data set (13,056 bp), topological constraint enforcing the most basal *Protanguilla* within the Anguilliformes: (Ne) sister group of (An+Se)
    d) $12_{n_r}3_rRT_n$ data set (13,056 bp), topological constraint enforcing monophyly of the non-synaphobranchid anguilliforms: (Ne) sister group of (An+Se)
4. Tang and Fielitz (2013), 20 eel families, two mitochondrial genes: topology based on best likelihood topology score:
    a) (Se) is sister group of (An+Ne).
5. Santini et al. (2013), 20 eel families, three nuclear and two mitochondrial genes: maximum likelihood tree based on ''concatenated dataset'':
    a) (Ne)+(Se+X) is the sister group of (An+X)
6. Chen et al. (2014), 13 eel families (Serrivomeridae not included), three nuclear and three mitochondrial genes, two maximum likelihood trees:
    a) based only on nuclear genes: (An) is sister group of (Ne+X)
    b) based on combined nuclear and mitochondrial genes: (Ne) is sister group of (An+X)

Our analyses of the preceding molecular studies suggest that Serrivomeridae, Anguillidae, and Nemichthyidae form a closely related group with all three permutations of their possible intrarelationships reported variously in those studies. Although, morphological studies have been basically uninformative, possibly because they only appeared to evaluate two of the families at one time (and because of the highly derived morphology of Serrivomeridae), we think that the molecular evidence suggests that a re-evaluation of the families, including a study of the gill-arch muscles of nemichthyids is in order, but not within our own priorities. That is why we included a description of the gill-arch muscles of *Serrivomer*. The only morphological evidence that *Serrivomer* might be closely related to *Anguilla* is that they are

the only two eels of those we report in Table 1 that share in having R2.

CONCLUSIONS

Johnson et al. (2012) presented morphological and molecular evidence that *Protanguilla palau* is an anguilliform eel, and proposed that the Protanguillidae represents the sister group of all other members of the Anguilliformes. Our comparative study of the gill-arch musculature of the Elopomorpha, including representatives of the eel families most commonly proposed as the most primitive, and *Serrivomer*, is summarized in Table 1. From it, we identify the following muscle character states as putative synapomorphies of the Anguilliformes:

1) Absence of LI3 (lost independently in Notacanthidae); first reported by S&J.
2) Presence of MPb2-Eb1 (lacking in *Synaphobranchus*, in which Pb2 has been reduced to a small cartilage). Reported for first time.
3) Absence of one of the two PCls that characterize almost all other teleosts (lost independently in Notacanthidae). Reported for the first time.
4) Presence of R3 and R4 (R2 also present only in *Anguilla* and *Serrivomer*). Reported for the first time.
5) Presence of at least RecD2 (of RecDs1–4, of which all four are present only in *Protanguilla*; all are absent only in the highly specialized *Simenchelys*). Reported for the first time.
6) Absence of RecCom. Reported for the first time.
7) LI2 insertion includes UP4. Although first noted as an anguilliform synapomorphy by S&J (p. 71, item 1, based on its presence in *Conger* and *Synaphobranchus* and absence in other elopomorphs), we confirm its important presence in *Protanguilla* and its absence in *Simenchelys*, in which it was erroneously indicated as present in S&J's table 2.

We also report for the first time two new anguilliform skeletal synapomorphies:

1) Hb3 is, uniquely among lower teleosts, either cartilaginous or absent in all Anguilliformes.
2) AC4, identified as Eb5 in the literature prior to 2013, is absent (lost independently in *Albula* and *Lipogenys*).

There is considerable homoplasy in the gill-arch musculature of anguilliforms. This is not surprising given the reductive trends that characterize their gill-arch skeletons. We have, however, identified two characters of the gill arches of *Protanguilla* (one myological, one osteological) that corroborate its primitive state and hypothesized placement as the sister group of other anguilliforms:

1) *Protanguilla* lacks R4Cm, which is present in all other eels for which the condition is known, except muraenids. Parsimony dictates that the muraenid condition is a secondary loss, perhaps not surprisingly, given that the gill arches of this family are highly reductively derived.
2) *Protanguilla* exhibits the primitive and most common teleostean configuration of the BB3, BB4, and Hb3 complex (not described, but illustrated in Johnson et al., 2012:fig. 3), wherein the Hb3s have narrowed extensions that extend well forward along each side

of the well-developed Bb3, which articulates tightly with a well-developed Bb4 and often has a posterior ''tail'' that extends below it. The appearance of this complex in *Protanguilla* is very similar to that in most other teleosts, including the elopomorphs, *Elops saurus* (CS, USNM 272928), *Megalops atlanticus* (CS, USNM 357435), *Aldrovandia*, *Polyacanthonotus*, and *Notacanthus* (Kanehira et al., 2012:fig. 13A, 14A, B), but not *Lipogenys*. In all other eels, the contralateral, ovoid to rectangular Hb3s meet (or approach each other) in the midline posterior to Bb3 and thus fully separate it from Bb4 (Bb3 and Bb4 are variously reduced in many eels).

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