

Clarification of the Occipito-Vertebral Region of *Arapaima gigas* (Osteoglossomorpha: Osteoglossidae) through Developmental Osteology

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The structure and composition of the ventral portion of the occipital region of the skull in *Arapaima gigas* (Osteoglossidae) is unique among teleostean fishes, and past comparative anatomical studies have variously interpreted it as containing only the basioccipital or the basioccipital fused to one or two vertebral centra. By studying an ontogenetic series, we show that the dominant element of the ventral occipital region of the skull in *Arapaima* is the first vertebral centrum and its greatly enlarged parapophyses. The parapophyses, which become fused to the centrum, extend anteriorly to suture to the lateral portions of the parasphenoid. In the adult, the anterior portion of the basioccipital is flattened, with a narrow ventrally directed keel of bone that is exposed ventrally only along the midline of the skull. Although a general enlargement of the anteriormost parapophyses appears to be a synapomorphy of the family Osteoglossidae, their arrangement in other osteoglossids does not closely resemble that described herein for *Arapaima*.

OSTEOGLOSSOMORPH fishes form one of the most basal groups of extant teleosts (Greenwood et al., 1966; Patterson and Rosen, 1977; Arratia, 1997). With the exception of the vast radiation of the African family Mormyridae (which contains more than 200 species), osteoglossomorph fishes are represented by relatively few extant taxa (ten non-mormyroid genera, several of which are monotypic), although there is an extensive fossil record (Li and Wilson, 1996a, Li et al., 1997a, b; Kumar et al., 2005; and references cited therein). The phylogenetic relationships within Osteoglossomorpha have been the subject of much recent study (Li and Wilson, 1996b; Taverne, 1998; Hilton, 2003). The members of this group retain many characteristics that are plesiomorphic for teleosts, although they are also highly derived fishes, many of which show peculiar and unique features of anatomy (Nelson, 1969). One such member is the Pirarucú or Paiche (*Arapaima gigas*) from the Amazon River basin, the sole representative of the genus.

Arapaima is widely regarded as the sister-group of the monotypic African genus *Heterotis*, and together they are classified with the arowanas (*Osteoglossum* and *Scleropages*) in the family Osteoglossidae (Nelson, 1968; Hilton, 2003; Lavoué and Sullivan, 2004). *Arapaima* is one of the largest completely freshwater fishes in the world, reaching lengths of at least 390 cm (Ferraris, 2003; reports of larger individuals are considered unreliable, Eigenmann and Allen, 1942:339) and is perhaps also one of the most distinctive. Because of this distinctiveness and its phylogenetic position, there have been several osteological studies of *Arapaima* (Spix and

Agassiz, 1829; Ridewood, 1905; Taverne, 1977), although many aspects of its anatomy remain unknown, particularly with regard to the development of its skeleton.

Herein we describe the skeleton of *Arapaima gigas* at the boundary between the occipital region of the skull and the anterior portion of the vertebral column, with the goal of clarifying its composition through the study of its ontogeny. This region of *Arapaima* is particularly complex and unique among teleostean fishes, and has been variably interpreted in previous comparative anatomical studies.

MATERIALS AND METHODS

Specimens examined include both cleared-and-stained (Dingerkus and Uhler, 1977; Taylor and van Dyke, 1985) and dry skeletons. This material represents a broad range of sizes (19.5 mm SL to est. 1525 mm SL) and captures the first ossifications of some elements of this region of the skull, as well as the adult condition (although our largest specimen is less than half the length of the maximum size of this species). Institutional abbreviations used in the text follow Leviton et al. (1985) with the addition of UMA for University of Massachusetts Amherst Zoology Collection. Cleared-and-stained specimens were examined using Zeiss DRC or Wild M5 microscopes with substage illumination, and photographed digitally using a ProgRes C12 plus digital camera mounted on a Zeiss Tessovar, a Leica MZ75 microscope with a Spot Insight digital camera attachment, or a Nikon COOL-PIX 8700 coupled to a Wild M5 microscope. Adult material was photographed using the Nikon COOL-PIX,

and line drawings were rendered using Adobe Illustrator software.

RESULTS

In the smallest specimen available (INPA 22779; 19.5 mm SL; Fig. 1A), the vertebral centra are thinly ossified rings of bone and the first pair of parapophyses are small, weakly formed cartilages that are only lightly stained with alcian blue. However, they are clearly present and in series with the more posterior parapophyses, although positioned slightly more ventrally on the centrum. As in most other lower teleosts (Patterson and Johnson, 1995), Baudelot's ligaments (unlabeled and not clearly visible in Fig. 1) attach to the parapophyses of the first vertebra. Both the paired exoccipitals and the median basioccipital are well ossified at this stage and the perichordal ossification of the basioccipital is shaped like a cone with a broad circular posterior surface (i.e., centrum-like) that tapers anteriorly to a point and is slightly curved ventrally, demarcating the ventral contour of the neurocranium.

In later stages (e.g., Fig. 1B–D), the centra are more robustly ossified. The anteriormost parapophyses ossify and grow anteriorly to reach the level of the posterior margin of the basioccipital by 27.5 mm SL (Fig. 1B; at this stage, this anterior growth is slight and is best seen in lateral view, and therefore is not clear in Fig. 1C). At this size the basioccipital is still the dominant ossification of the ventral occipital region. The parapophyses continue to grow anteriorly, lateral to the basioccipital, and contact the parasphenoid at about the level of the anterior margin of the vagal foramen in the exoccipital by 55 mm SL (Fig. 1E). At this stage, the parapophyses remain autogenous from the centrum and the basioccipital. The basioccipital is still broadly exposed in the ventral midline, but is no longer curved ventrally and is flattened as it is in the adult.

The anteriorly directed parapophyses eventually fuse to the first centrum, at which time the adult condition is established (Fig. 2). A precise timing of these fusions is unknown given the specimens available, but they are definitely achieved by 145 mm SL (Fig. 1F), and Taverne (1977:figs. 125, 127) illustrated a 67-mm specimen that shows the adult configuration (confirmed by us). The parapophyses suture to the parasphenoid far forward on the skull, at about the level of the posterior margin of the tooth patch, anterior to the level of the prootic-exoccipital suture. The insertions of Baudelot's ligaments, however, are at the points of fusion between the parapophyses and the centrum (i.e.,

they do not migrate forward as the parapophyses grow anteriorly). The posterior surface of the basioccipital is concave (i.e., centrum-like), and the element as a whole is locked in place by the posterior processes of the parasphenoid ventrally, the hypertrophied parapophyses laterally, and the first centrum posteriorly. The basioccipital remains visible in ventral view as an elongate keel of bone that is flush with the ventral surface of the occipital region and is exposed only between the posterior processes of the parasphenoid (Fig. 2). Taverne's (1977) illustration suggests that the basioccipital and first vertebral centrum are fused in his specimen (although see Taverne, 1980). However, we observed a clear separation between the basioccipital and the first centrum in all of our specimens with the exception of one of the largest individuals examined (Fig. 3), in which the two are fused at the "centrum-like" surface of the basioccipital, whereas the anterior portion of this element (i.e., the flattened ventral surface) is definitely free from the parapophyses. The significance of this fusion (i.e., ontogenetic or individual variation) is difficult to interpret because in specimens of roughly equivalent size as that shown in Fig. 3, the two elements are separate.

DISCUSSION

That the occiput of *Arapaima* is distinctive in its form has long been appreciated (Spix and Agassiz, 1829:34; "*talis articulatio atlantis cum cranio nusquam in toto regno animali . . .*;" "this type of articulation between the atlas and the skull is found nowhere else in all the animal kingdom . . ."), and is one of the features used to identify *Arapaima*, or at least *Arapaima*-like specimens, in the fossil record (Lundberg and Chernoff, 1992; Gayet and Meunier, 1998). However, considerable confusion has persisted in the literature concerning the occipito-vertebral arrangement in *Arapaima*, perhaps stemming from the fact that the first vertebra has paired anteriorly directed lateral processes (i.e., the parapophyses) that intimately suture with the parasphenoid, much like the basioccipital in other teleosts.

Spix and Agassiz (1829:Anatomical Plate B, fig. 4) illustrated the first vertebra in isolation and described its peculiar structure, with the two anteriorly directed processes (their *Atlas et ejus processus inferiores*) that suture with the parasphenoid (their *sphaenoideum principale*), leaving only a small part of the basioccipital exposed ventrally. In his classic study of the skull of osteoglossids, Ridewood (1905:265) stated that the "occipital half-centrum presents a shallow concavity be-

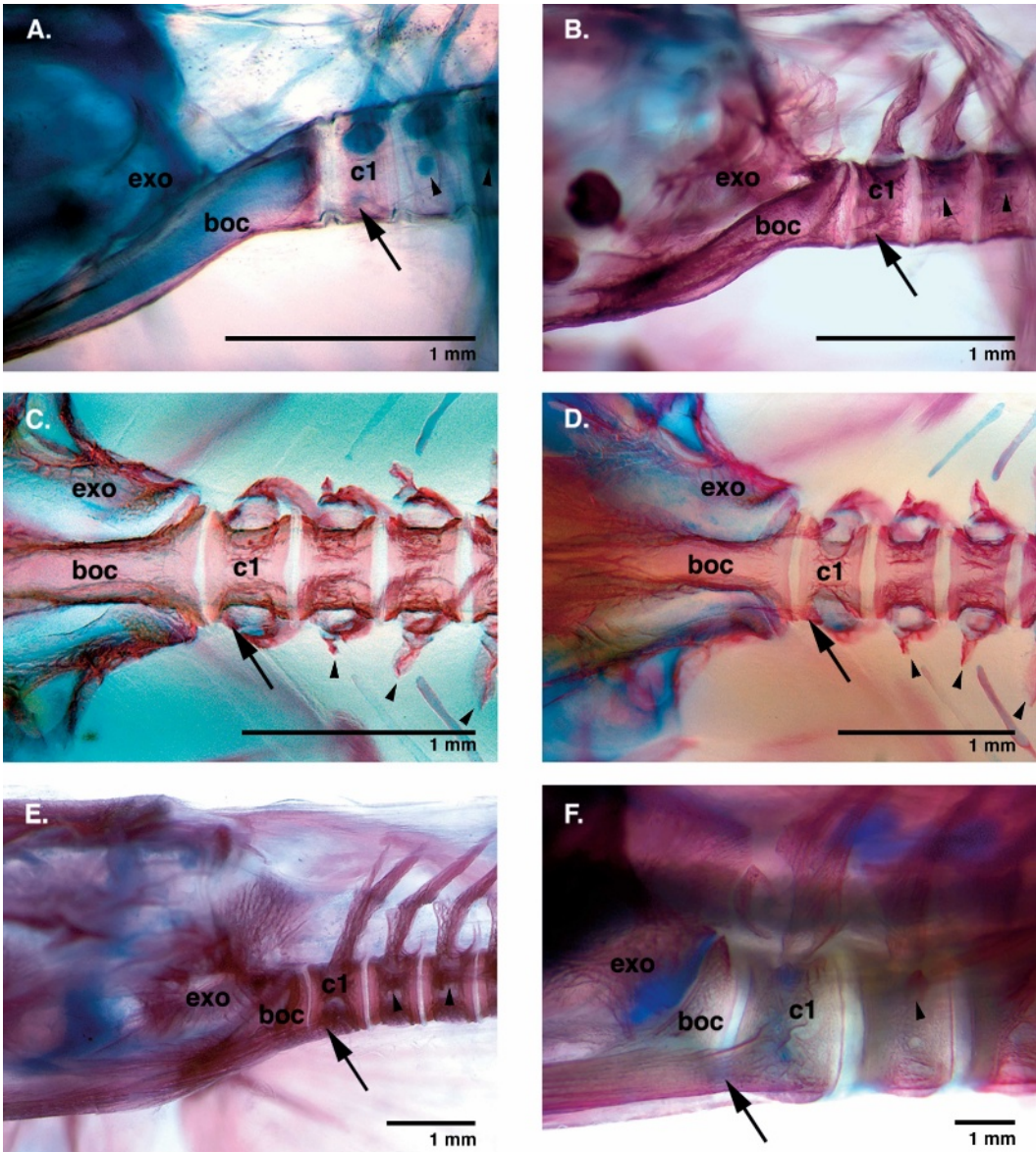


Fig. 1. The occipital region of *Arapaima gigas* at early stages of development, bone stained red, cartilage stained blue. (A) Lateral view; parapophysis unossified (INPA 22779; 19.5 mm SL). (B) Lateral view (INPA 22785; 27.5 mm SL). (C) Ventral view (ZFMK 1006–1028; 29.7 mm SL). (D) Ventral view (ZFMK 948–965; 63 mm SL). (E) Lateral view; parapophysis reaches far anterior but remains autogenous from the centrum (FMNH 97450; 56.5 mm SL). (F) Lateral view; parapophysis fused to centrum (UMA F11261; 145 mm SL). Arrows point to the first parapophysis; small arrowheads point to more posterior parapophyses. Note that Baudelot's ligaments and the myosepta are not clearly visible in this figure. Anterior to left (images in A, B, E, F reversed). Abbreviations: boc, basioccipital; c1, centrum 1; exo, exoccipital.

hind, and is readily separable from the basioccipital and exoccipital bones. The vertebral centrum behind this may also be regarded as a constituent of the cranium, since its lower portion is continued forward into two parallel processes, right and left, which are rigidly united

by long jagged sutures with the back of the parasphenoid." Although correct about the structure and relationships of the vertebra with the long anterior processes, we are unable to explain his confusion of the posterior part of the basioccipital with the first centrum (his "half-

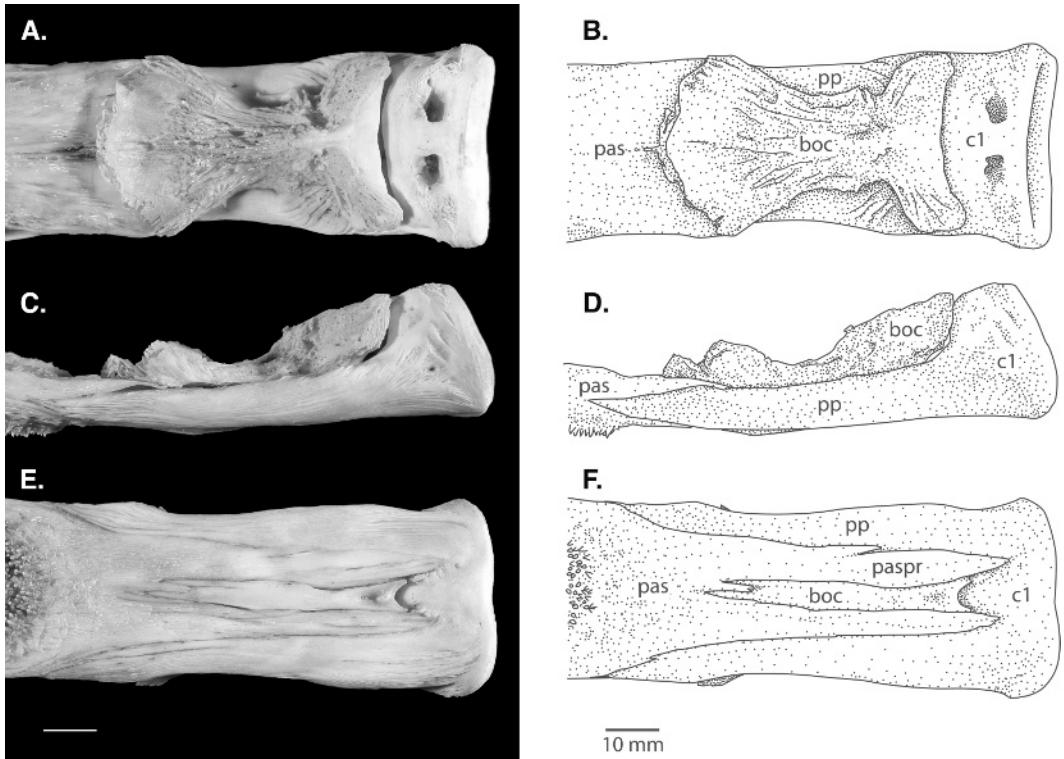


Fig. 2. Partially disarticulated occipital region of *Arapaima gigas* showing the typical arrangement of occipital bones in adult specimens (FMNH 99287; est. 1525 mm SL). (A, B) Dorsal view. (C, D) Lateral view. (E, F) Ventral view. This specimen was illustrated also by Lundberg and Chernoff (1992:fig. 3). Anterior facing left. Abbreviations: boc, basioccipital; c1, centrum 1; pas, parasphenoid; paspr, posterior process of parasphenoid (= basioccipital process of Hilton, 2003); pp, parapophysis.

centrum”). His interpretation, as well as that of subsequent authors, likely followed from the long held presumption that the occipital region of most teleostean fishes has incorporated the anteriormost centrum into the posterior portion of the basioccipital. However, recent study of the occipital region in actinopterygian fishes (RB and GDJ, pers. obs.), through study of ontogeny (when available) and the relationship between the skeleton and the myosepta and Baudelot’s ligament, provides no support for this claim (see also Patterson and Johnson, 1995:16–17).

Subsequent authors have concluded that the vertebra with the pair of long anterior processes is fused to the basioccipital, which, as we have shown above, is unfounded. For instance, Taverne (1977:213; fig. 125) thought that the basioccipital incorporated two vertebrae, the first giving rise to anterior ventral processes that come to cover the body of the basioccipital proper and are then, in turn, covered by similar processes of the second vertebra, both in turn fusing with the basioccipital “primitif.” Consequently, Taverne’s (1977) basioccipital included both the basiocci-

pital and the first vertebra with its anterior processes. We checked Taverne’s (1977) specimen and believe that he, as did Ridewood (1905), interpreted the posterior part of the basioccipital as including the first vertebra. He also commented on this region of the skull in a short note (Taverne, 1980:fig. 1.3) in which he illustrated the basioccipital as distinct, if not completely independent, from the “vertèbre crânienne” (= the first vertebra) and again noted that the basioccipital is fused to a vertebra that supports a neural arch.

Lundberg and Chernoff (1992:4) also concluded that the basioccipital complex of *Arapaima* “is a mosaic of the parasphenoid, the basioccipital proper, V1, and V2.” In their figure of the fossil specimen described in that paper (their fig. 2; unlabeled in their photos of *A. gigas*, fig. 3), they have the joint between the basioccipital and the first centrum labeled as the “v1–v2 joint” and the first centrum labeled as supporting the “v2–basioccipital sutures.” Therefore, it can be concluded that they considered the first centrum to be a fusion between the basioccipital

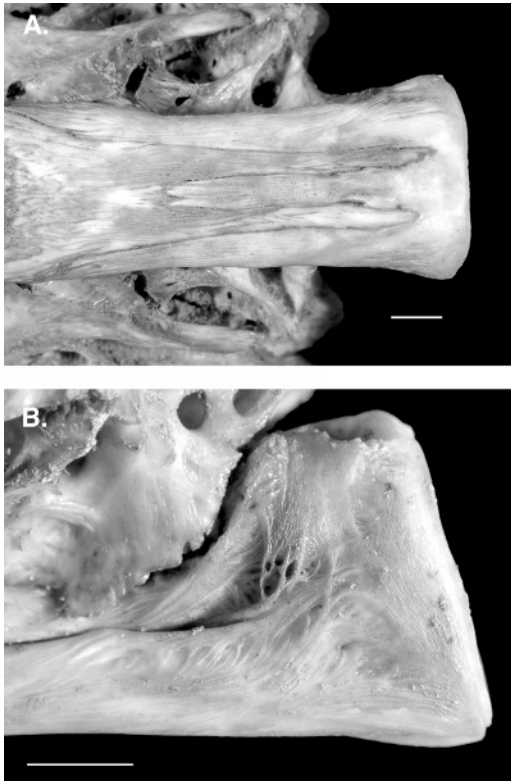


Fig. 3. The occipital region of *Arapaima gigas* showing fusion between the basioccipital and first centrum (FMNH 99286; est. 1500 mm SL); compare with Fig. 2. This is the only specimen examined in which these bones were found to be fused. (A) Ventral and (B) lateral views. Anterior facing left. Scale bars = 10 mm.

and the second centrum. Bemis and Forey (2001) similarly identified the basioccipital as the first centrum and identified the first vertebra as the basioccipital plus centrum 2. Hilton (2003:fig. 18) presented a different interpretation, labeling the first vertebra with the anterior processes as the basioccipital with no indication of the incorporation of any vertebral element. Through the study of its ontogeny, we have shown that the complexity of this region of the skull of *Arapaima* is achieved by the anterior growth of the parapophyses of the anteriormost vertebra to become intimately associated with the bones of the occipital region.

The specialization of the posterior portion of the skull in *Arapaima* adds to the elongation of its neurocranium and derived nature of its skull generally (Gregory, 1933). In particular, we note that the cranio-vertebral junction functionally has shifted from between the basioccipital and the first vertebral centrum, as it is in most basal

teleosts, to the joint between the first and second vertebrae.

Although *Arapaima* displays a unique arrangement of the occiput, this region of the skull is modified in other osteoglossids as well, albeit in different ways. For instance, *Heterotis* has been interpreted to have the first vertebra fused to the basioccipital, following from both ontogenetic (e.g., study of staged series; Daget and d'Aubenton, 1957) and topographic (e.g., relationship to Baudelot's ligament; Patterson and Johnson, 1995) lines of evidence. Other osteoglossids also have enlarged parapophyses on the first vertebra that contact the basioccipital and parasphenoid (e.g., †*Phareodus* and an undescribed fossil taxon; PLF and EJH, pers. obs.). The first parapophyses of *Osteoglossum* and *Scleropages*, which remain autogenous, are slightly enlarged and are of different shape than the more posterior ones. In these two taxa, the parapophyses straddle the joint between the basioccipital and first centrum (Taverne, 1977:fig. 62; pers. obs.), and Baudelot's ligament attaches to the anterior portion of the parapophyses, and then continues to attach also to the basioccipital. It is tempting to view the condition in *Osteoglossum* and *Scleropages* as a first step towards the consolidation of the articulation of the first vertebra with the skull seen in *Arapaima* by bridging the gap with the parapophyses. Although modified, however, the parapophyses in these taxa are not hypertrophied to the degree found in the fossil osteoglossids and certainly do not closely resemble the situation described above in *Arapaima*. Therefore, a general enlargement of the first parapophysis appears to be a synapomorphy of the family Osteoglossidae (PLF and EJH, pers. obs.), with subsequent modifications and, as yet unclear, phylogenetic patterns within its subgroups.

MATERIAL EXAMINED

The following specimens of *Arapaima gigas* were examined (standard lengths, SL, are given if known or could be estimated, est.; ds = dry skeleton, CS = cleared and stained): BMNH 1966.9.14.35 (1 CS; 67 mm, probably the specimen described in Taverne [1977]); FMNH 97450 (5 CS; 55–57 mm SL); FMNH 85741 (1 ds; est. 780 mm SL); FMNH 94750 (1 ds; est. 1120 mm SL); FMNH 72733 (1 ds; est. 1360 mm SL); FMNH 99286 (1 ds; est. 1500 mm SL); FMNH 99287 (1 ds; est. 1525 mm SL); INPA 22779 (1 CS; 19.5 mm SL); INPA 22785 (3 CS; 27.5–29.0 mm SL); UMA F11261 (1 CS; 145 mm SL); ZFMK 948–965 (2 CS; 63–65 mm SL); ZFMK 1006–1028 (4 CS; 29.5–32.2 mm SL). Skeletal specimens of other osteoglossid fishes (*Heterotis*,

Osteoglossum, *Scleropages*), including both cleared-and-stained juveniles and dried skeletal adult specimens, were also examined.

ACKNOWLEDGMENTS

This paper came about through a bit of happenstance. In an ongoing study of fossil and living members of Osteoglossidae, two of us (PLF and EJH) prepared and examined a growth series of *Arapaima* that was to be described in the context of the unusual arrangement of the occipital region discovered in an undescribed fossil taxon. At the same time, RB and GDJ also discovered the peculiar aspects of the development of the occipital region of *Arapaima* in an ongoing study of the composition of the occiput of teleostean fishes. In discussing the two collaborations, we realized that we had independently discovered the unique pattern of development in *Arapaima* and decided to combine our results and present this short paper. We thank J. Friel (CU), M. Westneat and M. A. Rogers (FMNH), L. Rapp Py-Daniel and L. Melo de Sousa (INPA), and W. Bemis (formerly of UMA) for loan of and permission to prepare specimens used in this study, and M. Kearney for access to her photomicroscopy equipment. EJH thanks NSF (DEB-0414552, to Hilton and Grande) and a Smithsonian Institution Postdoctoral Fellowship for support.

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