First Paleocene elopid fish (Teleostei, Elopiformes): *Landanaelops gunnelli* gen. and sp. nov. from the marine margin of the Congo Basin, Cabinda, Angola

by

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KEYWORDS. — Teleostei; Elopiformes; Paleocene; Landana; Cabinda.

SUMMARY. — The cranial osteology and the first vertebrae of *Landanaelops gunnelli* gen. and sp. nov., a fossil fish from the Paleocene strata of Landana (Cabinda Province, Angola), are described in detail. The characters of the skull indicate that this basal teleost belongs to the order Elopiformes and more particularly to the family Elopidae. Comparisons with other elopid fishes show that *Landanaelops* deserves a particular generic status. Nevertheless, the specialised morphology of the anterior margin of the orbit is an apomorphy shared with the Upper Cretaceous genus *Nardoelops* and the extant genus *Elops*.

MOTS-CLÉS. — Teleostei; Elopiformes; Paléocène, Landana, Cabinda.

RESUMÉ. — L'ostéologie crânienne et les premières vertèbres de *Landanaelops gunnelli* gen. et sp. nov., un poisson fossile des strates paléocènes de Landana (Province de Cabinda, Angola), sont décrites en details. Les caractères du crane indiquent que ce téléostéen basal appartient à l'ordre des Elopiformes et plus particulièrement à la famille des Elopidae. Des comparaisons avec d'autres poissons élopidés montrent que *Landanaelops* mérite un statut générique particulier. Néanmoins, morphologie spécialisée de la marge antérieure de l'orbite est une apomorphie partagée avec le genre *Nardoelops* du Crétacé supérieur et le genre actuel *Elops*.

TREFWOORDEN. — Teleostei; Elopiformes; Paleoceen; Landana; Cabinda.

SAMENVATTING. — De schedelosteologie en de eerste wervels van *Landanaelops gunnelli* gen. en sp. nov., een fossiele vis uit de Paleocene lagen van Landana (provincie

Cabinda, Angola), worden in detail beschreven. De kenmerken van de schedel geven aan dat deze basale teleost behoort tot de orde Elopiformes en meer in het bijzonder tot de familie Elopidae. Vergelijkingen met andere elopide vissen laten zien dat *Landanaelops* een bijzondere generieke status verdient. Niettemin is de gespecialiseerde morfologie van de voorste rand van de orbit een apomorfie die gedeeld wordt met het genus *Nardoelops* uit het Boven-Krijt en het huidige genus *Elops*.

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Introduction

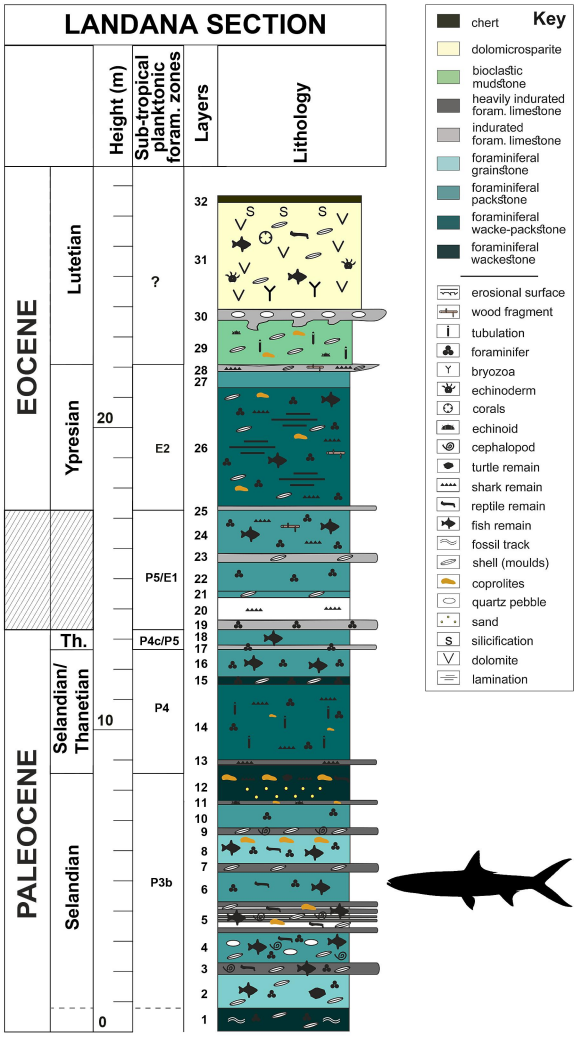
An important amount of various fossil specimens from Upper Cretaceous and Paleogene marine deposits was collected in the coastal region of the Lower Congo Basin and in the Cabinda Territory during the expeditions conducted by the naturalist Joseph Bequaert in 1913 and the paleontologist Edmond Dartevelle in 1933 and 1937-1938. The most productive of these expeditions was the one-year expedition of E. Dartevelle, from January 1937 to January 1938, which was notably supported by the Royal Belgian Colonial Institute (today the Royal Academy for Overseas Sciences).

The fossil fishes were particularly abundant in that material. They were described in four monographs (Dartevelle & Casier, 1943, 1949, 1959; Casier, 1960). Nevertheless, a few fish remains from that rich material were left undetermined or were not mentioned in those monographs. Two specimens belonging to that undescribed material were studied more recently, an osteoglossid caudal skeleton (Taverne, 2009, 2017) and an anterior half skeleton of a new chanid genus (Taverne *et al.*, 2019), both coming from the Paleocene strata of Landana in the Cabinda Province, Angola (Fig. 1).

A third undetermined specimen is an incomplete and crushed skull of a moderately large teleost also collected in the Paleocene section of Landana. This specimen was found in a pile of eight drawers belonging to the Royal Museum for Central Africa (Tervuren, Belgium), which were in loan for several decades at the Royal Belgian Institute of natural Sciences (RBINS). After the premature death of Edmont Dartevelle at the age of 49 in 1956, Edgard Casier continued the study of undescribed fish remains and requested the transfer of some of the collections to the RBINS. Even though Casier published many papers on African fishes, including his last paper in 1971, he never finished the study of the ichthyological material from the Bas Congo. The aim of this paper is to describe the third specimen referenced above and to determine its taxonomic relationships.

Geological and paleontological settings

The specimen here described was discovered in 1937 in the Landana cliff section, a marine Paleogene fossil site located in the Cabinda enclave, today a province of Angola. The Landana fossil site, currently located on the west African coast at 2 to 3 km south of the Shiloango river mouth (GPS coordinates: 05° 13’ S, 12° 07’ E; Fig. 1), forms part of the Paleogene marine margin of the Congo Basin (see Dartevelle & Casier, 1943, p. 48, fig. 23).



The lithological sequence of the Landana section (Fig. 2) has been subdivided into 32 sedimentary layers (named “couches” in Dartevelle & Casier, 1943). The bio- and chemostratigraphic context of these layers has recently been revisited to refine their age constraints and has revealed the almost complete absence of Danian deposits, contrary to prevailing interpretations for over than half a century (Solé *et al.*, 2019). The Danian is probably absent or reduced to a single layer (layer 1). The Landana section clearly includes the early Selandian (layers 2-12), the Thanetian (layers 13-18), the Thanetian-Ypresian transition (layers 19-24), the early Ypresian (layers 25-28), and the Lutetian (29-31). The layer 32 is a chert bed that might correspond to a major Lutetian denudation event in the Congo Basin (De Putter *et al.*, 2016).

Interestingly, the specimen described herein is one of the few finds for which the layer from which it came is not indicated on the specimen label. However, only a few layers have yielded fragmentary fish skeletons, namely layers 1, 3, 5, 8 and 10. Layer 1 has indeed

yielded a young individual of the scombroid *Landanichthys lusitanicus* (MRAC RG 9165; Dartevelle & Casier, 1959) and the chanid *Cabindachanos dartevelli* (MRAC RG 4629; Taverne *et al.*, 2019); layer 3 yielded the osteglossid *Ridewoodichthys caheni* (Taverne, 1969, 2017); layer 5 yielded the holotypes of *Landanichthys lusitanicus* (MRAC RG 4614; Dartevelle & Casier, 1949) and *Landanichthys moutai* (MRAC RG 4617; Dartevelle & Casier, 1949); layer 8 yielded *Landanichthys* sp. (MRAC RG 9166; Dartevelle & Casier, 1959); and layer 10 yielded a tail of an unnamed osteglossid fish (MRAC RG 9183; Taverne, 2017). All these layers are from the lower part of the Landana section. Therefore, the specimen is possibly Danian or more probably early Selandian in age (Planktonic foraminifera subzone P3B, Solé *et al*., 2019).

Material and methods

The material hereafter described belongs to the paleontological collections of the Royal Museum for Central Africa (MRAC, Tervuren, Belgium), Department of Geology. The specimen was observed with a stereomicroscope Leica MZ8. The drawings of the figures were made by the first author (L. T.) with a *camera lucida*. Pictures were taken with a digital camera after covering the specimen with ammonium chloride.

Anatomical abbreviations used in the text figures

AN	=	angular
ANT	=	antorbital
APAL	=	autopalatine
ASPH	=	autosphenotic
BO	=	basioccipital
BR	=	branchial bone
BRSP	=	gill raker (= branchiospina)
BSPH	=	basisphenoid
CBR 1	=	ceratobranchial 1
CLT	=	cleithrum
DETH	=	dermethmoid (= rostral)
DN	=	dentary

EBR 1-4	=	epibranchial 1 to 4
ECPT	=	ectopterygoid
EPI	=	epiotic (= epioccipital)
EXO	=	exoccipital
FR	=	frontal
HBR	=	hypobranchial
HYOM	=	hyomandibula
IC	=	intercalar
IORB 1-4	=	infraorbitals 1 to 4
MPT	=	metapterygoid
MX	=	maxilla
NA	=	nasal
NEUR	=	neural arch
NEUREP	=	neural spine
OSPH	=	orbitosphenoid
PA	=	parietal
PBR 3	=	pharyngobranchial 3
PMX	=	premaxilla
POP	=	preopercle
PRO	=	prootic
PS	=	parasphenoid
PSPH	=	pleurosphenoid (= pterosphenoid)
QU	=	quadrate
RART	=	retroarticular
SMX 1-2	=	supramaxillae 1 and 2
SOC	=	supraoccipital
SPI	=	spicular (= first suprapharyngobranchial)
ST	=	supratemporal (= scale bone, extrascapular)
V1-6	=	vertebrae 1 to 6
ant. a.	=	anterior ampulla chamber of the internal ear
br.	=	broken
ext. a.	=	external ampulla chamber of the internal ear
f. IV	=	foramen for the trochlear (= pathetic) nerve (IV)
f. X	=	foramen for vagus nerve (X)

f. XI, XII	=	foramens for the occipito-spinal nerves
f. m.	=	foramen magnum
l.	=	left
p. c. can.	=	conduct for the posterior semi-circular canal of the internal ear
post. a.	=	posterior ampulla chamber of the internal ear
r.	=	right
t. f.	=	temporal (postemporal) fossa
ut.	=	utricular fossa

Systematic paleontology

Division Teleostei Müller, 1845

Superorder Elopomorpha Greenwood *et al.*, 1966

Order Elopiformes Sauvage, 1875

Familly Elopidae Bonaparte, 1846

Genus *Landanaelops* gen. nov.

Type species. Landanaelops gunnelli gen. and sp. nov. (here designated).

Diagnosis. As for the species (monospecific genus)

Etymology. The generic name refers to the locality of Landana in the Cabinda Province (Angola) and to the genus *Elops*.

Species *Landanaelops gunnelli* gen. and sp. nov.

Diagnosis. Elopiform fish of moderate size that differs from all other known elopiforms by a quadratic process fused to the body of the quadrate, forming a bulky swelling on the ventral border of the bone and by a groove for the symplectic on the inner side of the quadrate. *Landanaelops gunnelli* is also characterised by the following combination of characters: dermethmoid (= rostral) autogenous; tubular nasal; medioparietal skull; large orbitosphenoid and pleurosphenoid; autosphenotic bearing the chamber for the anterior ampulla of the inner ear; median crest of the supraoccipital strongly reduced; palatine toothless; jaws bearing bands of minute teeth; maxilla moderately broad and rectilinear; lower jaw elongated,

prognathous, with a short symphysis; angular and retroarticular fused together; mandibular sensory canal enclosed within the dentary and the angular; antorbital pressed against the anterior border of the first infraorbital and excluded from the orbit margin; first infraorbital with a broad anterior dorsal process reaching the lateral border of the frontal and forming the anterior margin of the orbit (apomorphic character shared with *Nardoelops* and *Elops*); first vertebra strongly reduced, firmly sutured to the basioccipital and completely integrated into the braincase.

Etymology. The species name is given in homage to our late friend and colleague Dr. Gregg F. Gunnell (1954-2017), from the Duke University (North Carolina, U.S.A.), an eminent specialist of Paleogene mammals and partner of the project PalEurAfrica.

Holotype. Specimen MRAC RG 9184 (collected in 1937 by E. Dartevelle at Landana, Cabinda Province, Angola, early Selandian, early-middle Paleocene). The sample is composed of an incomplete skull and of the six first vertebrae. Length of the specimen: 96 mm. With such a skull length, the total length of the concerned specimen can be estimated around 55 cm.

Osteology

1. The skull (Figs 3-6)

The head is incompletely preserved and severely crushed. Parts of the ethmoid and frontal regions and of the upper jaw are missing. Some bones are disjoined from the others.

The dermethmoid (= rostral) is a wide autogenous plate-like bone. Neither traces of a rostral sensory commissure nor rostral ossicles are visible. The endochondral part of the mesethmoid, the lateral ethmoid and the vomer are not preserved. A short tubular nasal is present just above the premaxilla on the left side of the skull.

Large fragments of the two frontals and the right parietal are the only preserved region of the skull roof. The supraorbital and the otic sensory canals and a possible parietal sensory commissure are not visible. The parietal is a wide and square-like bone that meets the mid-line of the braincase. The skull is thus medioparietal. The supraoccipital is massive, with an extremely reduced and acuminate median crest. The posterior semi-circular canal of the inner ear is present on the internal side of the bone. The inner face of the left autosphenotic is visible on the right side of the skull. The bone bears the chamber for the anterior ampulla of

the inner ear. Only fragments of the left pterotic and the posterior region of the right pterotic are preserved. The temporal (= posttemporal) fossa is located on the rear of the skull and is surrounded by the epiotic, the pterotic and the exoccipital. A small intercalar is present but it does not reach the border of the temporal fossa. The supratemporal is displaced along the first vertebrae by the fossilization. It is a very large bone.

The orbitosphenoid, the pleurosphenoid and fragments of the basisphenoid and of the parasphenoid are preserved. The orbitosphenoid and the pleurosphenoid are rather large bones located above the orbit. Anteriorly, the orbitosphenoid is slightly swollen, forming a small knob. Posteriorly, the bone is divided in two long lateral wings. The pleurosphenoid bears the foramen for the trochlear nerve (IV). The ventral face of the parasphenoid is not accessible and it is not possible to know if it bore teeth.

The inner side of the right prootic is visible on the left side of the skull. Anteriorly, the bone bears a large utricular fossa and, posteriorly, the chamber for the external ampulla of the inner ear. The two exoccipitals surround the *foramen magnum*. Two small foramina for the occipito-spinal nerves (XI, XII) are pierced in the rear side of the bone. The large foramen for the vagus nerve (X) is hidden below a small wing-like lateral process of the exoccipital. The basioccipital is firmly sutured to the strongly reduced first vertebra. The two bones form conjointly the articular condyle for the second vertebra.

The palatine is a small but robust bone. It is devoid of teeth. The ectopterygoid is long and narrow. It bears a row of small dental alveoli. The entopterygoid is not preserved. Both the quadrate and the metapterygoid are large bones. The quadrate is triangular, with a strong articular condyle. The inner face of the left quadrate is visible on the right side of the skull. There is a groove for the symplectic near the ventral margin of the bone. The quadratic process is not separated from the quadrate body but is represented by a bulky swelling of the ventral border. This swelling has an acuminate posterior extremity.

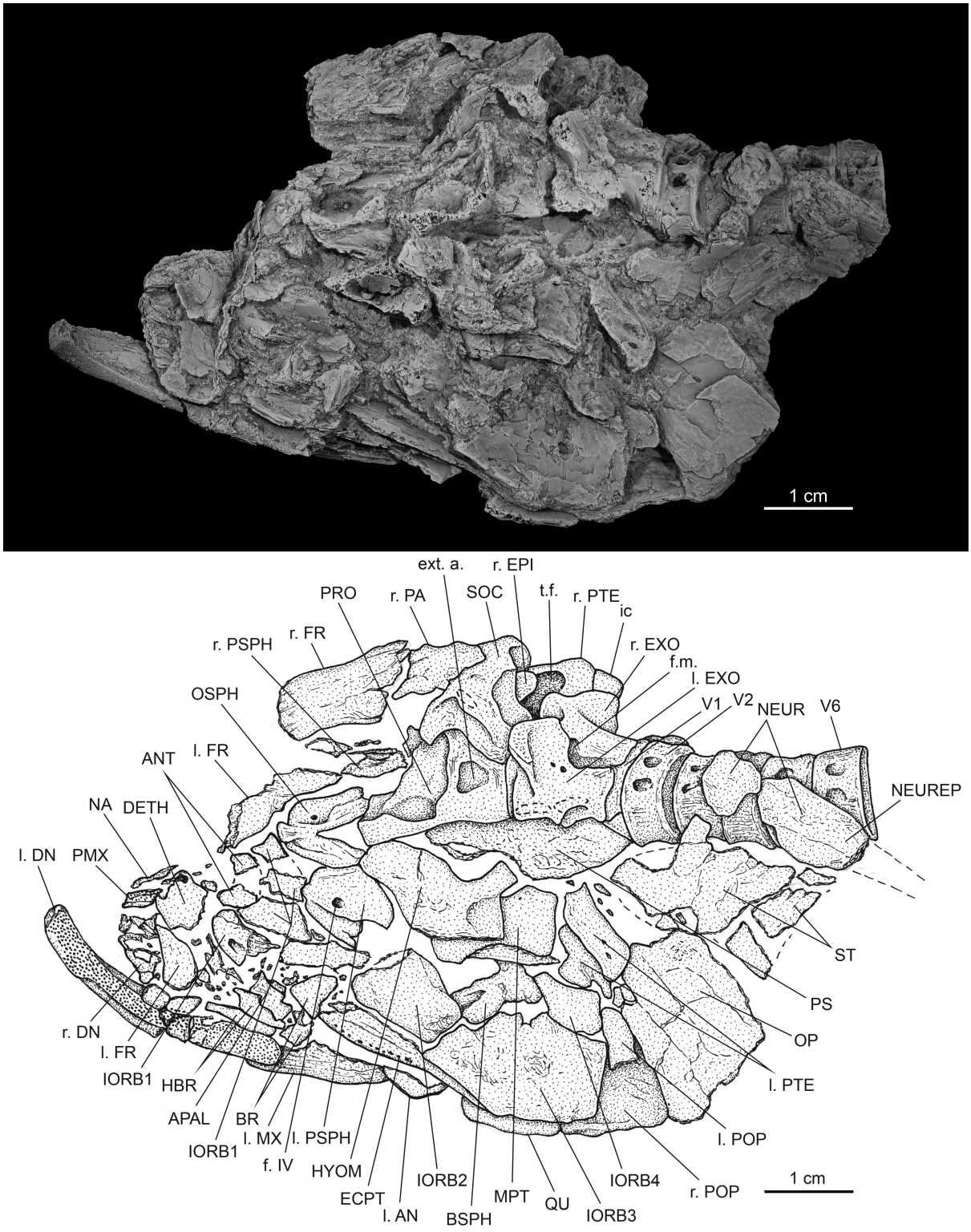
Parts of a premaxilla are visible on the left side of the skull. A long fragment on the right maxilla is also preserved. The bone is moderately broad and almost rectilinear. Both the premaxilla and the maxilla bear a band of small dental alveoli. There are two supramaxillae. The first one is small, with a pointed anterior extremity and a rounded posterior region. The second one is a large bone that partly overlaps the first one. The lower jaw is slightly prognathous and extends posteriorly far behind the orbit. The dentary is narrow in the symphyseal region, but it rises up rapidly toward the back of the bone. The oral margin of the dentary bears a long patch of dental alveoli like those of the premaxilla and the maxilla. The angular and the retroarticular are fused together. The articular is not visible. The mandibular

sensory canals are enclosed in the dentary and the angular, but some rare small openings are visible all along its length.

The circumorbital bones are preserved on the left side of the skull. The antorbital and the first infraorbital are broken into several elements. The antorbital is arched and pressed against the anterior border of the first infraorbital. This last bone is a large one. Its anterior region bears a broad ascending process that reaches the lateral margin of the frontal, forming so the anterior border of the orbit. The antorbital does not participate to this orbital border. The second infraorbital is almost as deep than long. The third infraorbital is by far the wider of the series. The fourth infraorbital is smaller. The fifth infraorbital, the dermosphenotic, the supraorbital and any possible sclerotic bones are not preserved. The infraorbital sensory canal is not visible.

A part of the dorsal branch of the left preopercle and the inner side of the ventral region of the right preopercle are visible. The opercle is wide, deeper than long, with a straight anterior margin and a slightly curved posterior border. Fragments of at least five long and narrow branchiostegal rays are present. The subopercle, the interopercle and possible gular plate are not preserved.

The upper region of the hyomandibula is visible on both sides of the skull. The articular head of the bone is divided in two condyles. The opercular process is strongly developed. There is a large foramen for the *truncus hyoideomandibularis* of the facial nerve (VII).



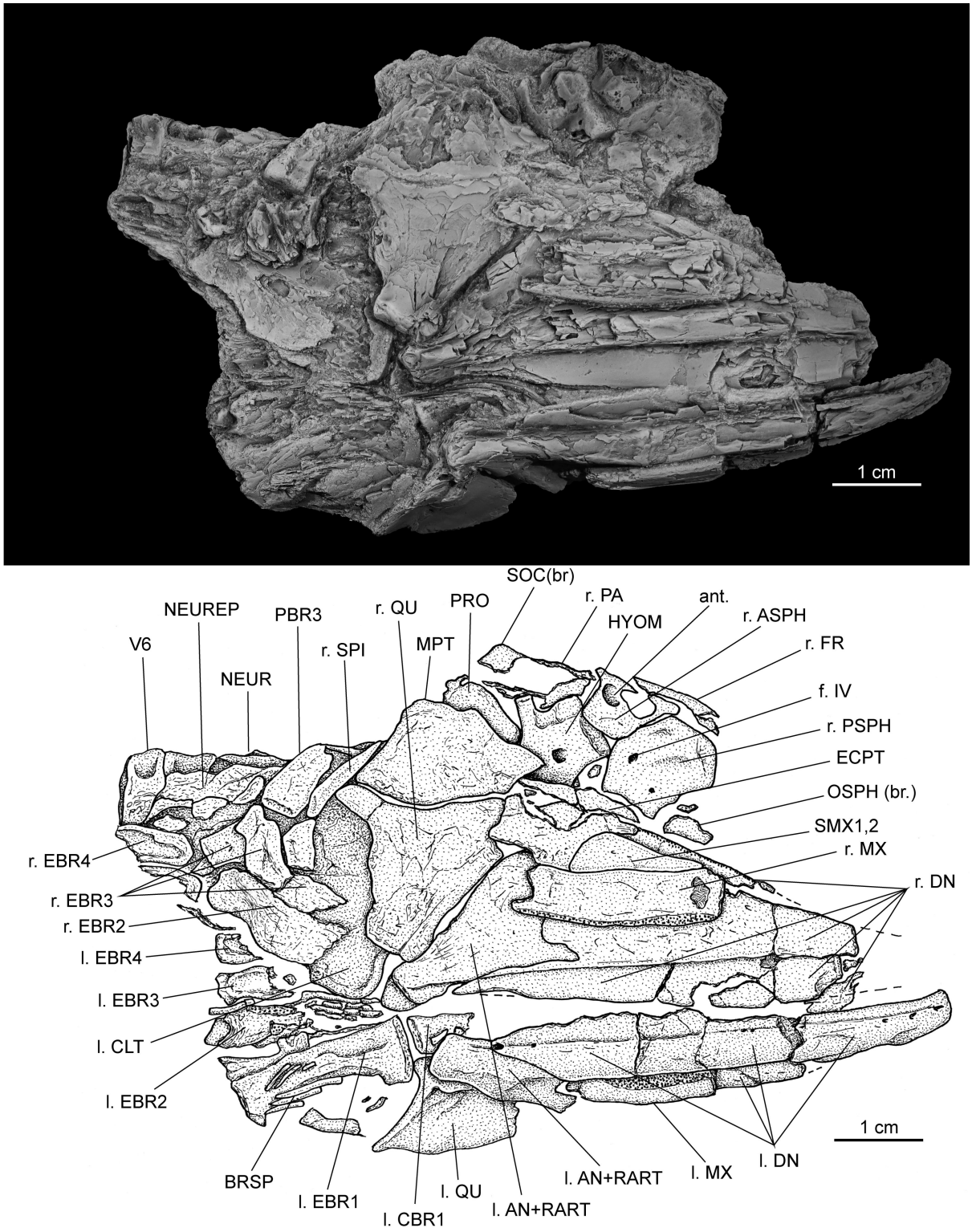
2. The branchial skeleton (Fig. 3)

An important portion of the branchial skeleton is visible on the right side of the specimen. The posterior region of the left first ceratobranchial, the complete left first epibranchial, fragments of the left second, third and fourth epibranchials, the complete right second epibranchial, fragments of the right third and fourth epibranchials, the right

suprapharyngobranchial and the right third pharyngobranchial are preserved. The first suprapharyngobranchial is rod like, with an acuminate dorsal extremity. The third pharyngobranchial is a massive element. The left second epibranchial bears two fragments of a plate covered by small dental alveoli. A few gill rakers are also visible. They are long, thin, and not denticulated.

3. The pectoral girdle (Fig. 3)

A great part of the inner face of the left cleithrum is visible on the right side of the skull. The other elements of the pectoral girdle are not present.



4. The axial skeleton (Figs 3, 4)

The first sixth vertebrae are preserved. The first vertebra is strongly reduced, intimately sutured to the basioccipital and completely integrated in the braincase. The other vertebrae are disc-like, with a pair of small dorsal fossae for the articulation of the neural arches. A part of two neural arches is also preserved.

Discussion

Determine the systematic position of a fossil fish when an incomplete and crushed skull is practically the only part that is preserved is a challenge. However, the cranial and vertebral remains of *Landanaelops* exhibit some features allowing to precise the relationships of that new genus.

The following characters attest that *Landanaelops* is a basal teleost (Arratia, 1997, 1999; de Pinna, 1996; among others). The dermethmoid is a large autogenous bony lamella. The skull is medioparietal and the parietal is rather large. The orbitosphenoid and the basisphenoid are present and well developed. The oral border of the upper jaw is principally formed by the maxilla. There are two well-developed supramaxillae. The supratemporal is a large bone. The temporal fossa is covered and located on the rear of the braincase.

Two other apomorphies refer more particularly this African fish to the superorder Elopomorpha. Both jaws indeed bear a large band of very small teeth and the angular and the retroarticular are fused together.

At least three other characters allow to place *Landanaelops* in the Elopiformes rather than in their sister-group the Albuliformes. The new African genus has a slightly prognathous snout, with an elongate lower jaw that protrudes relative to the premaxilla and the dermethmoid, these two bones being a little posteriorly located. The mandibular sensory canal is entirely enclosed in the bones of the lower jaw. The first vertebra is reduced and firmly integrated in the skull. Albuliform fishes show contrasting conditions: the snout is rather short, with frequently an inferior mouth; the mandibular sensory canal runs in an open groove; and the first vertebra is articulated to the basioccipital.

The order Elopiformes contains two families, the Elopidae and the Megalopidae, both lineages being represented by fossil and recent fishes. Other families, often monogeneric, were created within the order, such as the Anaethalionidae, the Protelopidae or the Sedenhorstiidae but their validity is questioned (Taverne, 1999).

The dermethmoid of *Landanaelops* is a thin plate-like bone. The maxilla is rather narrow and almost rectilinear. The lower jaw is elongated. The dentary symphysis is short. These four plesiomorphic characters are present in Elopidae (Forey, 1973a: figs 3, 6; Taverne, 1974: figs 1, 2; among others). Megalopidae exhibit more derived characters. They have the dermethmoid fused to the underlying endochondral mesethmoid. This massive bony element is articulated with the lateral ethmoid and delimits the boundaries of a rounded olfactive fossa (Forey, 1973a: figs 23, 30; Taverne, 1999: figs 3, 4). They have a shorter lower jaw, a deeper

dentary symphysis and a broader arched maxilla (Forey, 1973a: figs 24, 26, 32; Taverne, 1999: fig. 2; among others). *Landanaelops* is thus more similar to Elopidae than to Megalopidae.

Landanaelops exhibits a particular apomorphy. The first infraorbital bears a wide antero-dorsal process located just behind the antorbital and reaching the lateral border of the frontal. So, the anterior margin of the orbit is formed by the first infraorbital, the antorbital being excluded from this border. Within Elopidae, this specialized feature is shared by two other members of the family, *Elops* Linnaeus, 1766, a genus today represented by seven species (Nelson, 2016) and continuously present since the early Eocene but maybe already present from the Upper Jurassic of Germany (*Elops*-like sp.1 in Arratia, 1997: 47-56) and *Nardoelops* Taverne & Capasso, 2012 from the Upper Cretaceous of Italy (Forey, 1973b: fig. 6; Taverne, 1974: fig. 1; Taverne & Capasso, 2012: figs 5, 9). No other elopiform fish has this derived character. A comparison of *Landanaelops* with these two genera is thus necessary to establish the generic validity of the new African fossil fish.

Nardoelops is a toothless genus (Taverne & Capasso, 2012: fig. 6) and thus markedly differs from *Landanaelops*.

A few differences also exist between the skulls of *Landanaelops* and of *Elops*. In *Landanaelops*, the orbitosphenoid and the pleurosphenoid are large bones located above the orbit. The autosphenotic bears the chamber for the anterior ampulla of the inner ear. The palatine bone is toothless. The quadratic process is fused to the body of the quadrate. There is a groove for the symplectic on the internal face of the quadrate. In *Elops*, on the contrary the orbitosphenoid and pleurosphenoid are small bones positioned at the posterior region of the orbit, the chamber for the anterior ampulla is located on the prootic, the palatine is toothed, the quadratic process is separated from the body of the quadrate and the symplectic is fitted between the quadrate and the quadratic process (Forey, 1973a: fig. 3; Taverne, 1974: figs 2, 4, 11, 13, 15, 17) .

Landanaelops clearly differs from *Elops* and *Nardoelops* and therefore deserves its own generic status.

It is to be noted that *Landanaelops gunnelli* represents only the second occurrence of an elopiform fish in the Paleocene, the first one being *Protarpon boualii* Khalloufi *et al.*, 2018, a megalopid from the Danian strata of the Ouled Abdoun Basin, in Morocco (Khalloufi *et al.*, 2018). Albuliformes, the sister-order of the Elopiformes, are also represented by two species in the Paleocene, *Phosphonatator oxyrhynchus* Cavin *et al.*, 2000, also from the Moroccan Ouled Abdoun Basin, and *Farinichthys gigas* Gallo & De Figueiredo, 2002, from the

Pernambuco-Paraiba Basin of Brazil (Cavin *et al.*, 2000; Gallo & De Figueiredo, 2002). Nevertheless, *Landanaelops gunnelli* represents the first occurrence of an Elopidae in the Paleocene. It is not the first occurrence of a fossil elopid in that area of western Central Africa. Another elopid fish, *Kipalelops lepersonnei* Taverne, 1976, is known from the Upper Cretaceous of the Democratic Republic of Congo (Kipala, Kwango) and is represented by a caudal skeleton and a few scales (Taverne, 1976: figs 18, 19).

Although elopids are diverse in Upper Cretaceous strata, most of them extinct by the end of the Cretaceous. The discovery of *Landanaelops gunnelli* in the early-middle Paleocene of western Central Africa is therefore important as it fills the gap that existed between the Cretaceous elopids and the first ones from the Eocene.

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Text-figures

Fig. 1 – Map of the coastal region in the area of the Congo River mouth with the location of Landana in the Cabinda Province, Angola.

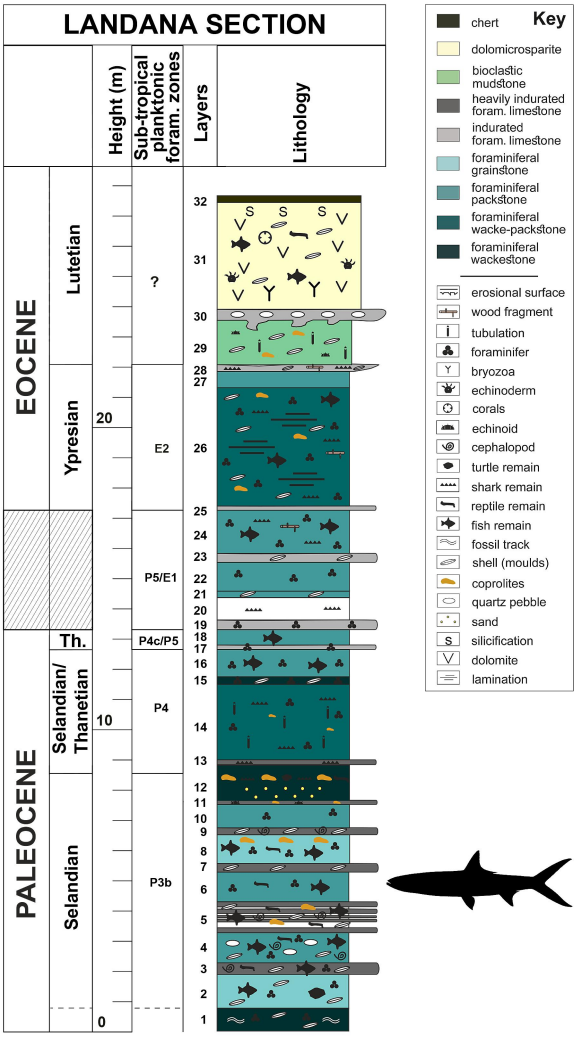

Fig. 2 – Stratigraphic log of Landana with the location of the new elopid fish *Landanaelops gunnelli* in early Selandian layers (modified from Solé et al., 2019).

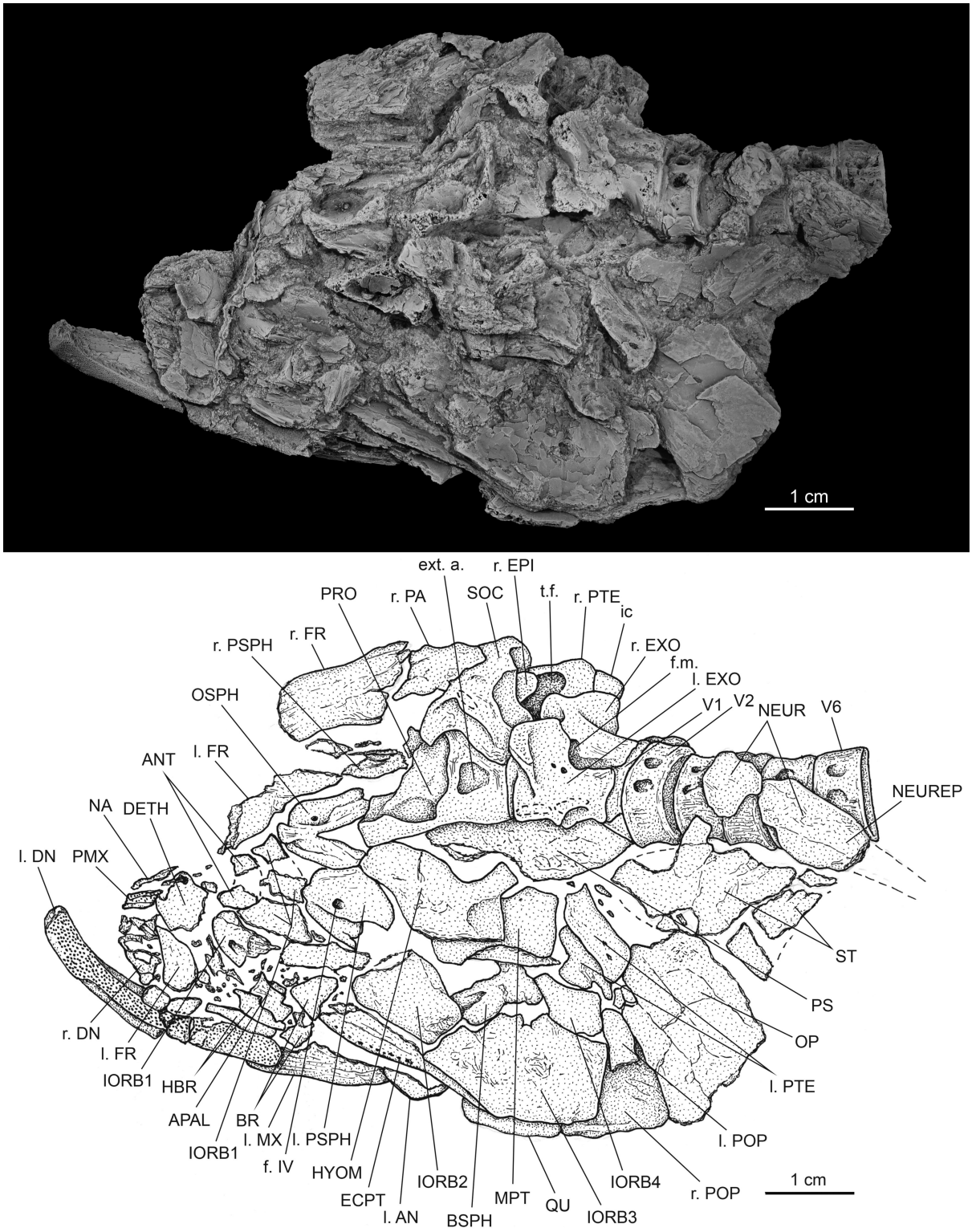

Fig. 3 – *Landanaelops gunnelli* gen. and sp. nov. Holotype MRAC RG 9184, right side. Photo (above) and drawing (below).

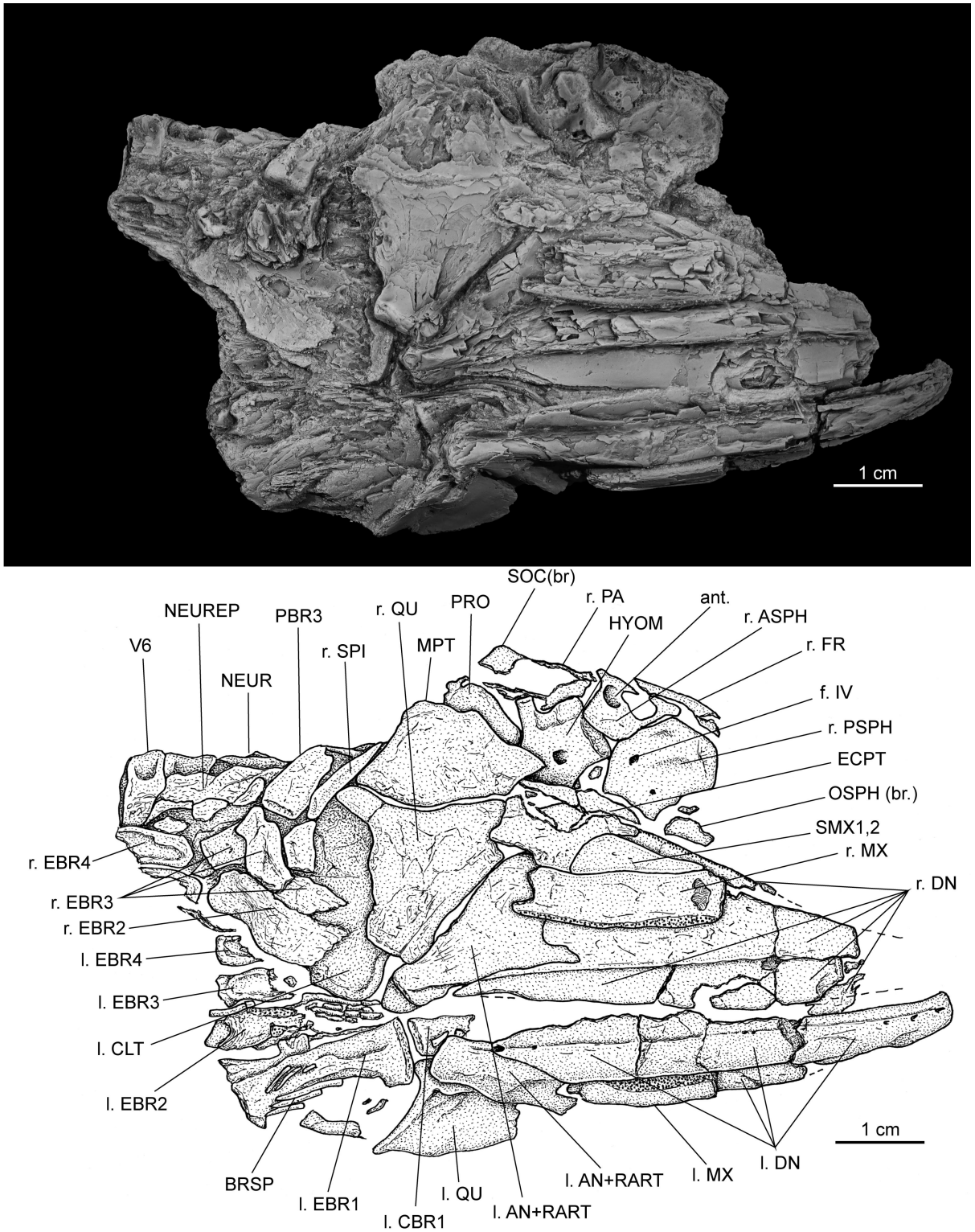

Fig. 4 – *Landanaelops gunnelli* gen. and sp. nov. Holotype MRAC RG 9184, left side. Photo (above) and drawing (below).

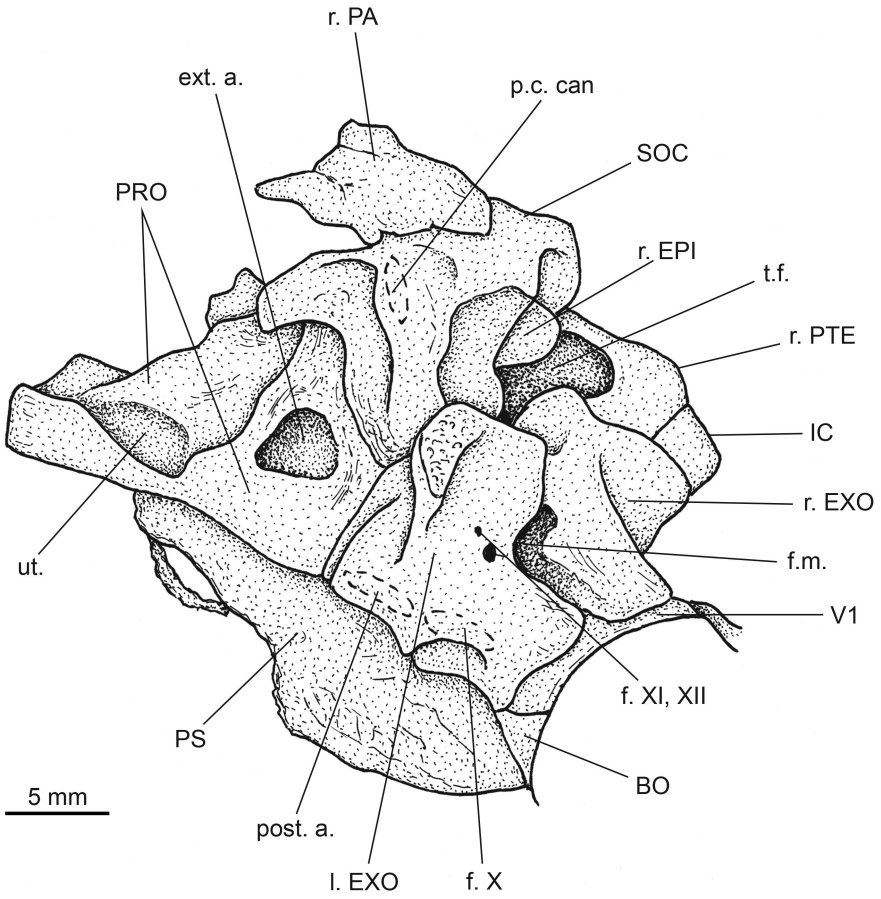

Fig. 5 – *Landanaelops gunnelli* gen. and sp. nov. Holotype MRAC RG 9184. The posterior region of the braincase (left side).

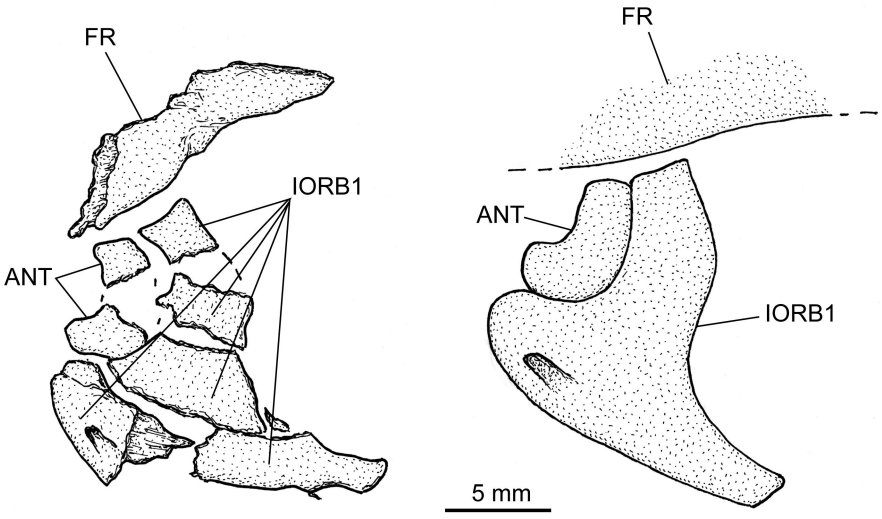

Fig. 6 – *Landanaelops gunnelli* gen. and sp. nov. Holotype MRAC RG 9184. Antorbital and first infraorbital in place (left) and reconstructed (right).