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FURTHER MOLECULAR IDENTIFICATION CONFIRMS THE OCCURRENCE OF *LAGOCEPHALUS GUENTHERI* MIRANDA RIBEIRO, 1915 IN THE AEGEAN COASTAL WATERS OF GREECE

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ABSTRACT

The occurrence of the diamondback puffer Lagocephalus guentheri Miranda Ribeiro, 1915 in the Greek waters of the Aegean Sea is herein confirmed through DNA barcoding based on a 608 bp fragment of the mitochondrial COI gene of a specimen collected on 14 September 2025 along the northwest coast of Rhodes Island, southeastern Aegean Sea, Greece. Morphological traits are evaluated alongside molecular data, with all nucleotide sequences used in the phylogenetic analysis consistently supporting the identification of L. guentheri. The present study aims to clarify the existence of this species in the region and to contribute additional reference sequences to public databases.

Key words: Nucleotide sequence, genetic identification, non-indigenous fish, Tetraodontidae, Eastern Mediterranean

ULTERIORE IDENTIFICAZIONE MOLECOLARE CONFERMA LA PRESENZA DI *LAGOCEPHALUS GUENTHERI* MIRANDA RIBEIRO, 1915 NELLE ACQUE COSTIERE GRECHE DELL'EGEO

SINTESI

La presenza del pesce palla Lagocephalus guentheri Miranda Ribeiro, 1915 nelle acque greche del mar Egeo viene confermata attraverso il DNA barcoding basato su 608 frammenti del gene mitocondriale COI di un esemplare raccolto il 14 Settembre 2025 nelle acque della costa nordoccidentale dell'isola di Rodi, mar Egeo sudorientale, Grecia. Le caratteristiche morfologiche vengono descritte mentre tutti i dati molecolari usati per l'analisi filogenetica confermano con certezza l'identificazione di L. guentheri. Lo studio ha lo scopo di chiarire l'esistenza della specie nella regione e di fornire ulteriori sequenze alle banche dati.

Parole chiave: sequenze nucleotidiche, identificazione genetica, pesci non-indigeni, Tetraodontidae, Mediterraneo orientale

INTRODUCTION

Among the 10 Tetraodontidae species present in the Mediterranean, including the questionable *Lagocephalus spadiceus* (Richardson, 1845), seven occur with certainty in the Greek waters of the Aegean Sea, namely the native *Lagocephalus lagocephalus* (Linnaeus, 1758), the non-indigenous from the Indo-Pacific/Red Sea (Lessepsian migrants) *Lagocephalus guentheri* Miranda Ribeiro, 1915, *Lagocephalus suezensis* Clark & Gohar, 1953, *Tylerius spinosissimus* (Regan, 1908), *Lagocephalus sceleratus* (Gmelin, 1789) and *Torquigener hypselogeneion* (Bleeker, 1852), and finally the range-expanding from the Atlantic *Sphaeroides pachygaster* (Müller & Troschel, 1848) (Corsini *et al.*, 2005; Papaconstantinou, 2014; Vella *et al.*, 2017; Giusti *et al.*, 2019; Kovačić *et al.*, 2021; Deidun *et al.*, 2024).

With the exception of the rarely encountered and small-sized *T. spinosissimus*, the other four non-indigenous tetraodontid species recorded in the Greek Aegean Sea have colonized the eastern Mediterranean coastal waters to varying degrees of population density, depending on the species. Some have expanded as far as the central Mediterranean, while the highly invasive, highly toxic, and large-sized *L. sceleratus* has impressively crossed the Sicily Channel westward, reaching the Strait of Gibraltar within just two decades of its first record in 2003 (Akyol *et al.*, 2005; Golani, 2021).

Among the above non-indigenous tetraodontids, *L. guentheri*, *L. suezensis* and *T. spinosissimus* are considered established in the Greek Aegean waters, while *L. sceleratus* and *T. hypselogeneion* are considered invasive (Zenetos *et al.*, 2024).

The Lessepsian migrant *L. guentheri* is native to the Red Sea and the Indo-West Pacific Ocean, from South Africa, Madagascar and Persian Gulf east to India, Indonesia northwestern Australia and the South China Sea and as north as southern Japan (Golani & Fricke, 2018; Froese & Pauly, 2025).

In the Greek coastal waters, *L. guentheri* was first recorded from Samos, North Aegean Sea as *Tetrodon spadiceus* Richardson, 1845, in 1952 (Ananiadis, 1952). Subsequent records came from Kos Island in 2007 (specimen preserved under the number HSR92 at the collection of the Hydrobiological Station of Rhodes, Hellenic Centre for Marine Research, HSR/HCMR), from Rhodes Island in 2008 (both reported as *L. spadiceus*; Corsini-Foka, 2010), from off Paralia Dikellon, Evros, North Aegean in 2007 (Evangelopoulos *et al.*, 2024; Zenetos *et al.*, 2024), and from off Pachi, Megara Gulf, Attica, western Aegean in 2017 (Kleitou *et al.*, 2018). Following the revision of the taxonomic status and distribution of *L. guentheri* by Matsuura *et al.* (2011), the earlier records of *L. spadiceus* previously reported in the Greek coastal waters were re-evaluated and subsequently considered misidentifications of *L. guentheri* (Corsini-Foka *et al.*,

2015; Zenetos *et al.*, 2017, 2018, 2024). Consistently, a specimen collected in 2016 from Crete and genetically identified as *L. spadiceus* was later reassigned to *L. guentheri* (Giusti *et al.*, 2019).

Records of the species throughout the Mediterranean, including the first from Israel in 1949, come from Egypt, Libya, Lebanon, Syria, Cyprus, Mediterranean and Aegean waters of Turkey and Malta; as *Tetrodon spadiceus* Richardson, 1845 (Kosswig, 1950; Ben-Tuvia, 1953), as *L. spadiceus* (Ali, 2018), as *Sphaeroides spadiceus* (Richardson, 1845) (Por, 1978); as *L. guentheri* (Iglésias & Frotté, 2015; Akyol & Aydın, 2016; Farrag *et al.*, 2016; Golani & Fricke, 2018; Bariche & Fricke, 2020; Deidun *et al.*, 2024; Zenetos *et al.*, 2024).

Due to the extreme similarities and only slight differences between *L. guentheri* and *L. spadiceus*, the significance and high importance of combining the proper distinguishing morphological characters (Matsuura *et al.*, 2011; Psomadakis *et al.*, 2015) with molecular data has been stated and thoroughly discussed in recent scientific literature (Turan *et al.*, 2017; Vella *et al.*, 2017; Giusti *et al.*, 2019; Deidun *et al.*, 2024).

Proper identification of *Lagocephalus* species occurring in the study area is fundamental to determining the current population status of *L. guentheri*, thereby, this study provides baseline data necessary to evaluate its potential invasiveness and related ecological and socio-economic impacts.

MATERIAL AND METHODS

On 14 September 2025, during a fisheries survey, an individual of Tetraodontidae was acquired by the first author from a fisher at the dock of Kremasti Village, located at the northwest coast of Rhodes Island (36.41867°N, 28.11655°E). Recreational rod-and-line angling was being performed by the fisher from the dock, at an approximate depth of less than 3 m using handmade bread dough as bait. The individual had been left on the dock, exposed to the sun and heat for approximately 1-2 hours. It was then transported to the facilities of the Hydrobiological Station of Rhodes (HSR) for meristic characters and morphometric measurements and identification based on key features described by Matsuura *et al.* (2011), Matsuura (2022) and Psomadakis *et al.* (2015) and other relevant publications that focus on the morphological differences of the two most likely species our individual resembled, namely *L. guentheri* and *L. spadiceus* (Giusti *et al.*, 2019; Deidun *et al.*, 2024). After preservation in the fridge at 4°C, the following morning photographs were taken with a Nikon AW111 camera and tissue sampling for DNA analysis was performed. The specimen (Fig. 1) and the tissue sample were fixed in 70% and absolute ethanol respectively, and the former was registered in the HSR collection with a Voucher number HSR.VOUCHER.579.

Genetic identification of the specimen was carried out using DNA barcoding. Genomic DNA was isolated from the sampled muscle tissue using the QIAamp DNA Mini Kit (Qiagen, Hilden, Germany), according to the manufacturer's protocol. A partial region of the mitochondrial cytochrome c oxidase I (COI) gene was amplified with the primers FISHCOILBC_ts and FISHCOIHBC_ts (Handy *et al.*, 2011). PCR amplifications were performed in a 30 µL reaction containing 1× PCR buffer, 2.5 mM MgCl₂, 0.2 mM dNTPs, 0.4 µM of each primer, 1 U Taq DNA polymerase, and 50–100 ng of template DNA. Thermal cycling consisted of an initial denaturation at 94 °C for 3 min, followed by 35 cycles of 95 °C for 40 s, 49 °C for 40 s, and 72 °C for 40 s, with a final extension at 72 °C for 5 min. PCR products were examined on 2% agarose gels and subsequently sequenced by GENEWIZ Germany GmbH (part of Azenta Life Sciences). The sequence was deposited to BOLD Systems database (Sample ID: HSR.DNA.041).

A total of 12 nucleotide sequences were included in the phylogenetic analysis; KY130423, KR861535, KY176508, PP338021, KM538365, KF442241, HQ149858, LC155438, HQ167726, EU595160 and KP266858. Sequences were aligned and trimmed to a final length of 590 bp. Phylogenetic relationships were inferred using the Maximum Likelihood (ML) method. The best-fit nucleotide substitution model was selected based on model testing in MEGA (Tamura *et al.*, 2023), using information criteria. The Kimura 2-parameter (K2) model was identified as the optimal model, with Bayesian Information Criterion (BIC) = 2645.47, Akaike Information Criterion (AIC) = 2494.58, and log-likelihood (lnL) = -1225.22. This model was subsequently applied for ML tree construction. Node support was assessed using

non-parametric bootstrap analysis with 1000 replicates. Bootstrap values were mapped onto the consensus ML tree to evaluate the robustness of inferred clades. The resulting phylogenetic tree was visualized and edited for presentation in FigTree (Rambaut, 2018).

RESULTS AND DISCUSSION

The meristic characters of the specimen under study were D 12, A 11, P 16 and C 13 all included within the range of the values D 12 - 14, A 11 - 12, P 16 - 19, C 13 - 17, cumulatively provided in published literature (Matsuura *et al.*, 2011; Psomadakis *et al.*, 2015; Akyol & Aydin, 2016; Erguden *et al.*, 2017; Kiparissis *et al.*, 2018; Golani *et al.*, 2021; Deidun *et al.*, 2024). Proportions of measurements expressed as % of standard length (Tab. 1) were compared and agreed with published literature (Appendices 1 and 2).

In agreement with Fig. 2 in Matsuura *et al.* (2011) and Psomadakis *et al.* (2015), a rhomboidal spinule patch on the back extending posteriorly to the region dorsal to the posterior part of the pectoral fin but not extending to dorsal fin origin, was clearly observed on our specimen. The length from snout to the posterior-most spinule was 53.16 mm whereas the distance from snout to dorsal fin origin was 80.05 mm (Tab. 1).

As far as the colour is concerned, while fresh, the specimen had a clear slightly lunate caudal fin with white upper and lower tips and traces of a medial posterior projection, as described in Matsuura *et al.* (2011), Matsuura (2022) and Psomadakis *et al.* (2015). Nevertheless, a slight differentiation of the caudal fin was apparent. The dorsal 2/3 of the caudal fin was brownish yellow while the ventral 1/3, apart from



Fig. 1: *Lagocephalus guentheri* Miranda Ribeiro, 1915, from the northwestern waters of Rhodes, southeastern Aegean Sea, Greece. Scale bar: 1 cm.

Sl. 1: *Lagocephalus guentheri* Miranda Ribeiro, 1915, iz severozahodnih voda Rodosa, jugovzhodno Egejsko morje, Grčija. Merilo: 1 cm.

Tab. 1: Morphometrics of *Lagocephalus guentheri* specimen from northwest coast of Rhodes Island, southeastern Aegean Sea, Greece. SL = standard length.

Tab. 1: Morfometrične meritve primerka vrste *Lagocephalus guentheri* s severozahodne obale otoka Rodos, jugovzhodno Egejsko morje, Grčija. SL = standardna dolžina.

Measurements	mm	SL %
Total length	143.2	
Standard length	134.5	
Head length	41.43	30.80
Snout length	19.54	14.53
Snout to dorsal-fin origin	80.05	59.52
Snout to anal-fin origin	85.57	63.62
Body depth at pectoral-fin base	38.11	28.33
Body depth at anal-fin origin	27.63	20.54
Depth of the caudal peduncle	8.08	6.01
Length of caudal peduncle	31.31	23.28
Gill opening length	10.62	7.90
Eye diameter	10.94	8.13
Bony interorbital width	15.51	11.53
Snout to nasal organ	13.91	10.34
Nose to eye	6.20	4.61
Length of dorsal-fin base	13.23	9.84
Length of anal-fin base	10.60	7.88
Longest dorsal-fin ray	23.25	17.29
Longest anal-fin ray	21.41	15.92
Longest pectoral-fin ray	21.09	15.68
Caudal-fin length	32.36	24.06

the white tip, had a blackish/white hue throughout its length (Fig.1), characters that could be attributed to *L. spadiceus* according to Matsuura *et al.* (2011), the illustrations in Psomadakis *et al.* (2015) and as pointed out in Giusti *et al.* (2019).

However, the observed differentiations, most likely a discoloration, may have resulted from the prolonged exposure of our specimen to the sun and atmospheric conditions leading to a loss of freshness, or from color variation within the species. The latter represents a well-documented theme in fish evolution and ecology, with numerous studies reporting geographically structured, population-level color differentiation. Such variation is often associated with differences in habitat and light environment, as well as with sexual selection,

predation pressure, or genetic drift, e.g. in *Coris julis* (Linnaeus, 1758) (Fruciano *et al.*, 2011) and pufferfishes (Yamanoue *et al.*, 2009).

Overall morphological examination revealed that the specimen most probably belonged to the species *L. guentheri*. Since issues with the identification of *L. spadiceus* and *L. guentheri* in the Mediterranean have previously been highlighted (Turan *et al.*, 2017; Vella *et al.*, 2017; Deidun *et al.*, 2024), we considered it necessary to confirm the identity of the individual through DNA barcoding. Molecular analysis, indeed, provided an unequivocal validation, assigning the specimen to the species *L. guentheri* (Fig. 2).

The Maximum Likelihood phylogenetic analysis based on 590 bp nucleotide sequences resolved the relationships among the analyzed *Lagocephalus* taxa with strong statistical support (Fig. 2). The resulting tree clearly separated the sequences into three well-supported clades corresponding to *L. guentheri*, *L. spadiceus* and *Lagocephalus cheesmanii* (Clarke, 1897).

All sequences identified as *L. guentheri*, following the corrections by Giusti *et al.* (2019) for sequences KY130423, KR861535 and KM538365, clustered together in a monophyletic clade (haplogroup α ; Giusti *et al.*, 2019) with high bootstrap support (100%). This clade included reference sequences from Greece, Lebanon, Turkey, Malta, Israel, India, and Iran, as well as our specimen, which grouped within the *L. guentheri* cluster, confirming its species-level identification. A second strongly supported clade (bootstrap value = 100%) corresponded to *L. spadiceus* (haplogroup β ; Giusti *et al.*, 2019) and comprised sequences originating from Japan, Turkey, and China.

An earlier DNA confirmation of *L. guentheri* in the under-study area (SE Aegean Sea), could have been possible based on the archived specimen HSR92 mentioned above (as *L. spadiceus*; Corsini-Foka, 2010). However, the latter, although later morphologically identified as *L. guentheri* following Matsuura *et al.* (2011), was no further involved in the present study as it was preserved for many years in formaldehyde, a substance not suitable for prolonged preservation prior to DNA analysis.

The present study provides unequivocal confirmation of the occurrence of *L. guentheri* in the Aegean Sea coasts of Greece through the combined application of detailed morphological examination and mitochondrial COI barcoding. Although minor colour-pattern deviations were observed, the specimen's meristic and morphometric characters were consistent with the diagnostic features of *L. guentheri*, while molecular analysis yielded clear phylogenetic placement within the species. These findings further corroborate previous evidence that historical Mediterranean records of *L. spadiceus* largely represent misidentifications of *L. guentheri*, underscoring the persistent taxonomic challenges posed by the close resemblance of these taxa. By contributing a vouchered specimen and a validated DNA sequences to public databases,

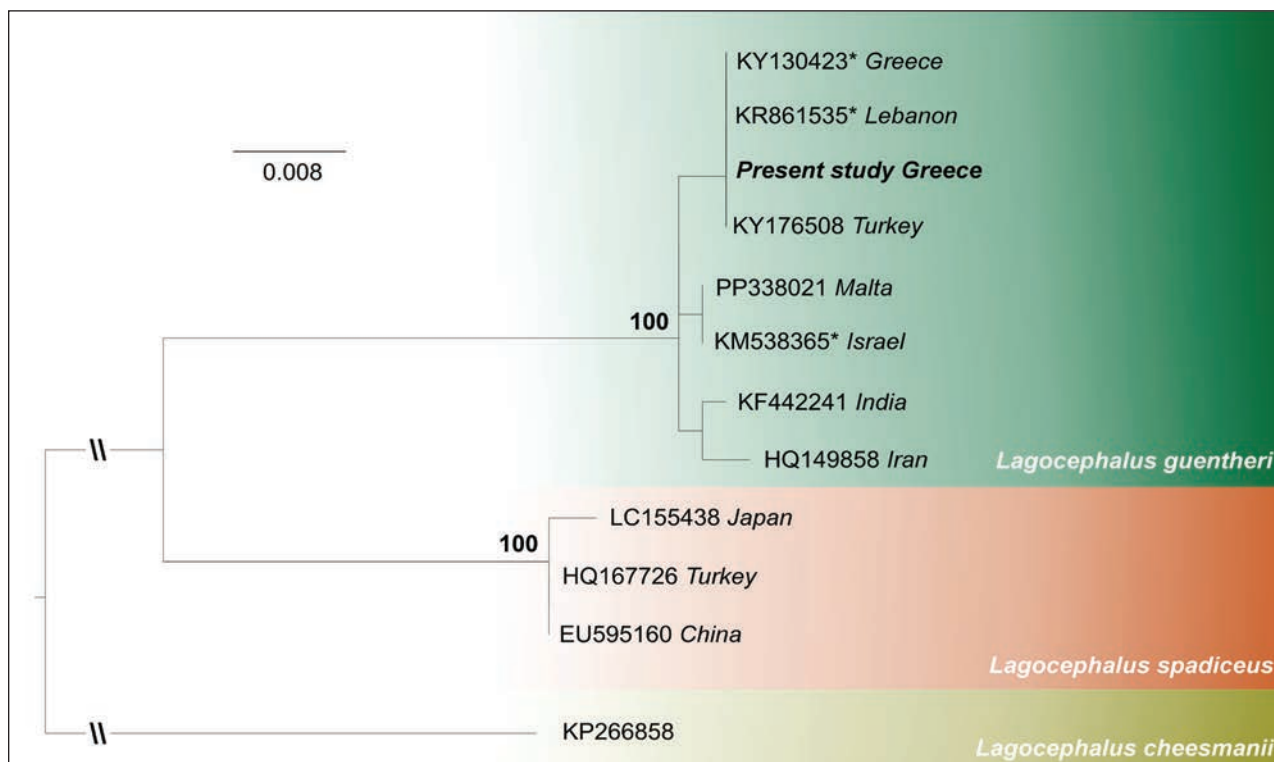


Fig. 2. Maximum-likelihood phylogenetic tree based on a 590 bp fragment of mitochondrial COI gene of *Lagocephalus* species. The analyzed specimen (in bold) clusters within the *Lagocephalus guentheri* clade, together with reference sequences from the Mediterranean and Indo-Pacific regions. *Lagocephalus spadiceus* and *L. cheesmanii* form well-supported, distinct clades. Bootstrap support values are shown at the nodes. Scale bar indicates genetic distance (substitutions per site). Asterisks refer to originally misidentified specimens.

Sl. 2: Najbolj verjetno filogenetsko drevo, ki temelji na 590 bp dolgem fragmentu mitohondrijskega gena COI vrst iz rodu *Lagocephalus*. Analizirani primerki (v krepkem tisku) se združujejo znotraj klada *Lagocephalus guentheri*, skupaj z referenčnimi zaporedji iz sredozemske in indo-pacifiške regije. *Lagocephalus spadiceus* in *L. cheesmanii* tvorita dobro podprte, ločene klade. Vrednosti podpore bootstrap so prikazane na vozliščih. Merilna vrstica označuje genetsko razdaljo (zamenjave na mesto). Zvezdice se nanašajo na prvotno napačno identificirane primerke.

this study enhances the reliability of reference material for the genus and supports recent assessments documenting the ongoing westward expansion of *L. guentheri* in the Mediterranean. The results reinforce the necessity of integrating morphological criteria with molecular tools in the accurate identification of non-indigenous pufferfishes, a prerequisite for reliable biogeographic assessments, biodiversity monitoring, and effective management of toxic species in Mediterranean waters.

CONCLUSIONS

The present study confirms the occurrence of *Lagocephalus guentheri* in the Aegean Sea coasts of Greece through the combined use of morphological examination and mitochondrial COI region. Although slight colour-pattern deviations were observed, the meristic and morphometric characters of the examined specimen were consistent with published diagnostic features of the

species, while molecular analysis provided unequivocal species-level validation. These findings further support the view that previous records of *L. spadiceus* from Greek waters largely refer to misidentified *L. guentheri*. By contributing a vouchered specimen and a validated DNA sequences to public databases, this study improves the reliability of reference material for *Lagocephalus* in the Mediterranean and highlights the importance of integrating morphological and molecular approaches for the accurate identification and monitoring of non-indigenous pufferfishes.

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NADALJNJA MOLEKULARNA IDENTIFIKACIJA POTRJUJE PRISOTNOST VRSTE
LAGOCEPHALUS GUENTHERI MIRANDA RIBEIRO, 1915 V EGEJSKIH OBALNIH
VODAH GRČIJE

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POVZETEK

Avtorji potrjujejo pojav zlate napihvalke Lagocephalus guentheri Miranda Ribeiro, 1915 v grških vodah Egejskega morja z DNK barkodiranjem na podlagi 608 bp dolgega fragmenta mitohondrijskega gena COI primerka, odvzetega 14. septembra 2025 ob severozahodni obali otoka Rodos v jugovzhodnem Egejskem morju v Grčiji. Morfološke lastnosti so ocenjene skupaj z molekularnimi podatki, pri čemer vsa nukleotidna zaporedja, uporabljena v filogenetski analizi, dosledno podpirajo identifikacijo L. guentheri. Namen pričujoče raziskave je potrditi pojavljanje te vrste v regiji in prispevati dodatne referenčne sekvence k javnim podatkovnim bazam.

Ključne besede: nukleotidne sekvence, genetska identifikacija, tujerodne ribe, Tetraodontidae, vzhodno Sredozemlje

Appendix 1: Published morphometrics of *Lagocephalus guentheri* holotype and specimens from the Mediterranean and the Red Sea. Priloga 1: Objavljene morfometrične značilnosti holotipa *Lagocephalus guentheri* in osebkov iz Sredozemlja in Rdečega morja.

Reference	Ananiadis (1952)	Matsuura (2011) Holotype		Matsuura <i>et al.</i> (2011)		Akyol & Aydin (2016)	Ergüden <i>et al.</i> (2017)		Vella <i>et al.</i> (2017)		Kiparisis <i>et al.</i> (2018)		Kleitou <i>et al.</i> (2018)		Deidun <i>et al.</i> (2024)		Present Study	
		mm	SL%	mm	SL%		mm	SL%	mm	SL%	mm	SL%	mm	SL%	mm	SL%	mm	SL%
Location	NW Samos Isl., south Aegean Sea			Brazil	Red Sea	Çandarlı Bay, Turkey	Iskenderun Bay, Turkey		NE Mediterranean	South Crete	off Pachi, Attiki, central Aegean Sea	Birzebbuga, Marsaxlokk Bay, island of Malta	Kremasti, Rhodes Island, southeastern Aegean sea					
Year of record	1952	1848	1972, 2009	2011	2015	2017	<2017	2016	2017	2023	2025							
Measurements	mm	SL%	mm	SL%	mm	SL%	mm	SL%	mm	SL%	mm	SL%	mm	SL%	mm	SL%	mm	SL%
Total length	185				134	337	167-194	202	239	270	143.2							
Standard length (SL)	155	175	117-183		114	289	135-159	172	206	223	134.5							
Head length	46.02	29.69		30.5-32.6	33	28.9	48.8-55.6	51.2	29.76	70	31.39	41.43	30.80					
Snout length (pre-orbital length)				15.4-16.6	14	12.3	17.1-20.7	22.6	13.14	29.7	13.32	19.54	14.53					
Snout to dorsal fin origin (pre-dorsal fin length)				63.0-67.5	71	62.3	96.3-107.4	109	63.60	145	65.02	80.05	59.52					
Snout to anal fin origin (pre-anal fin length)				64.8-66.7	73	64.0	93.7-105.9	112	65.23	148	66.37	85.57	63.62					
Body depth at pectoral fin base				17.6-20.1						65	29.15	38.11	28.33					
Body depth at anal fin origin				18.5-20.3						49	21.97	27.63	20.54					
Depth of the caudal peduncle (minimum body depth)				5.4-6.2			8.0-9.3	9.5	5.52	12.9	5.75	8.08	6.00					
Length of caudal peduncle (from end of anal fin) (end of anal base to end of SL)				25.8-26.8				47.4	27.55	58	26.01	31.31	23.28					
Gill opening length				7.8-10.7						21.4	9.60	10.62	7.89					
Eye diameter (eye width)	13.78	8.89		8.1-9.5	10	8.77	13.0-15.2	11.2	6.51	16	7.17	10.94	8.13					
Bony interorbital width (interorbital distance/space)				10.8-13.5				26.1	15.17	29	13	15.51	11.53					
Snout to nasal organ				9.8-11.3						23.1	10.36	13.91	10.34					
Nose to eye				4.4-5.2						12.6	5.65	6.2	4.61					
Length of dorsal fin base				10.4-11.1				18.1	10.52	20.6	9.24	13.23	9.84					
Length of anal fin base (Anal Fin Base Length)				9.2-10.7				13.3	7.73	19.1	8.56	10.6	7.88					
Longest dorsal fin ray				16.1-19.3						36.5	16.37	23.25	17.29					
Longest anal ray (Anal Fin Length)				16.5-19.0				29.2	16.98	42.1	18.88	21.41	15.92					
Longest pectoral ray (Pectoral Fin Length - from dorsal insertion point to end of longest ray)				16.8-18.5				29.3	17.03	38	17.04	21.09	15.68					
Caudal fin length				21.6-24.8						45	20.18	32.36	24.06					

Appendix 2: Published meristics of *Lagocephalus guentheri* holotype and specimens from the Mediterranean and the Red Sea.**Priloga 2: Objavljene meristike holotipa *Lagocephalus guentheri* in osebkov iz Sredozemlja in Rdečega morja.**

Reference	Meristic parameters	Dorsal Fin rays	Anal Fin rays	Pectoral Fin rays	Caudal Fin rays
Ananiadis (1952)		12	11		
Matsuura <i>et al.</i> (2011) Holotype		14	12	19	
Matsuura <i>et al.</i> (2011) Red Sea Specimens		12 to 13	11	16 to 17	
Matsuura <i>et al.</i> (2011)		12 to 14	11 to 12	16 to 19	
Psomadakis <i>et al.</i> (2015)		12 to 14	11 to 12		
Akyol & Aydın (2016)		12	11	16	
Ergüden <i>et al.</i> (2017)		13	11	19	17
Kiparissis <i>et al.</i> (2018)		13	11	16	13
Deidun <i>et al.</i> (2024)		12	11	17	
Present Study		12	11	16	13
Range		12 to 14	11 to 12	16 to 19	13 to 17

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