

## Taxonomic revision and molecular phylogeny of *Pisa* (Decapoda: Majoidea: Epialtidae), including the description of a new genus of Pisinae

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**Summary:** The spider crabs of the genus *Pisa* Leach, 1814 (Epialtidae: Pisinae) are reviewed in this study based on morphological and molecular data (16S and COI genes). From these results, a new genus, *Afropisa* n. gen., is established for the clade composed of *Pisa carinimana* Miers, 1879, *Pisa calva* Forest and Guinot, 1966 and *Pisa sanctaehelenae* Chace, 1966 based on carapace morphology, rostrum, pterygostomian tubercles and male gonopod 1. Additionally, *Lissa chiragra* (Fabricius, 1775) is transferred to *Pisa* based on morphological (adults and larvae) and molecular evidence. Furthermore, the status of *Pisa hirticornis* (Herbst, 1804) is discussed and clarified. The phylogenetic relationships between several Pisinae Dana, 1851 genera, as revealed by molecular data, are discussed. An illustrated identification key of eastern Atlantic and Mediterranean species of Pisinae is provided.

**Keywords:** *Afropisa* n. gen.; *Lissa chiragra*; morphology; illustrated key; *Pisa carinimana*, *Pisa calva*, *Pisa sanctaehelenae*, *Pisa hirticornis*.

**Revisión taxonómica y filogenia molecular de *Pisa* (Decapoda: Majoidea: Epialtidae), incluyendo la descripción de un nuevo género de Pisinae**

**Resumen:** Los cangrejos araña del género *Pisa* Leach, 1814 (Epialtidae: Pisinae) son revisados en este estudio basándonos en datos morfológicos y genéticos (genes 16S y COI). A partir de estos resultados, un nuevo género, *Afropisa* n. gen., es establecido para el clado compuesto por *Pisa carinimana* Miers, 1879, *Pisa calva* Forest and Guinot, 1966 y *Pisa sanctaehelenae* Chace, 1966 basado en la morfología del caparazón, rostro, tubérculos pterigostomianos y gonopodo 1 masculino. Además, *Lissa chiragra* (Fabricius, 1775) es transferida a *Pisa* basándonos en evidencias morfológicas (adultos y larvas) y moleculares. Adicionalmente, el estatus de *Pisa hirticornis* (Herbst, 1804) es discutido y clarificado. Se aporta una clave ilustrada de identificación para las especies de Pisinae Dana, 1851 del Atlántico oriental y del Mediterráneo.

**Palabras clave:** *Afropisa* n. gen.; *Lissa chiragra*; morfología; clave ilustrada; *Pisa carinimana*, *Pisa calva*, *Pisa sanctaehelenae*, *Pisa hirticornis*.

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## INTRODUCTION

*Pisa* Leach, 1814 currently comprises eight good species (WoRMS Editorial Board 2023, accessed 2023-06-23): *P. armata* (Latreille, 1803), *P. calva* Forest and Guinot, 1966, *P. carinimana* Miers, 1879, *P. hirticornis* (Herbst, 1804), *P. muscosa* (Linnaeus, 1758), *P. nodipes* Leach, 1815, *P. sanctaehelenae* Chace, 1966 and *P. tetraodon* (Pennant, 1777). The genus is distributed in the eastern Atlantic Ocean and in the Mediterranean Sea.

*Pisa* was established by Leach (1814: 431) for *Cancer biaculeatus* Montagu, 1813, a junior synonym of *Maja armata* Latreille, 1803. Later, Leach (1815: 50) described and added a new species, *Pisa nodipes*, to *Pisa*. H. Milne Edwards (1834) placed these two species under *Pisa* together with *P. tetraodon* (Pennant 177: 6), *P. armata*, *P. corallina* (currently considered a junior subjective synonym of *P. hirticornis*), *P. gibsii* Leach, 1815 (currently a junior subjective synonym of *P. armata*) and *P. styx* (described by Herbst 1803 as *Cancer styx*, but currently placed in the genus *Tylocarcinus* Miers, 1879). H. Milne Edwards also mentioned that *P. nodipes* seemed very close to *P. armata* and that *Cancer hirticornis* also belonged to the genus *Pisa*. However, the first species described belonging to *Pisa* was *Pisa muscosa* Linnaeus, 1758 (Linnaeus 1758: 628, as *Cancer muscosus*).

Risso (1816: 45) described *Maia corallina*, Lucas (1840: 137, 138) and, more recently, other authors (e.g. Zariquiey Álvarez 1968, d'Udekem d'Acoz 1999), considered it a good species as *Pisa corallina* (Risso, 1816). Currently, it is considered a synonym of *P. hirticornis* (Herbst, 1804) according to Sakai (1999).

Zariquiey Álvarez (1959) clarified the taxonomic position of *P. muscosa* in relation to *P. tetraodon* and *P. hirticornis*, using morphological characteristics, and Forest (1966) also gave a precise redescription of the three *Pisa* of the *tetraodon* complex.

Ng et al. (2008) considered a ninth species: *Pisa lanata* (Lamarck, 1801: 151), described as *Arctopsis lanata* with an extremely concise definition, but it is considered as a synonym of *P. armata* according to the WoRMS Editorial Board (2023) (see Remarks of *Pisa armata*).

The last three species described under the genus *Pisa* were *P. carinimana* by Miers (1879: 11–12), *P. sanctaehelenae* by Chace (1966: 651–654) and *P. calva* by Forest and Guinot (1966: 99–104), mainly distributed in African Atlantic waters. The close relationship between these species has already been pointed out by d'Udekem d'Acoz (1999). Furthermore, they exhibit some morphological features that put in doubt their generic placement. Consequently, this study is focused on the revision of *Pisa* species and allied genera, such as *Lissa* Leach, 1815 and *Micropisa* Stimpson, 1857, based on a re-examination of their morphological characters according to the phylogenetic relationships revealed by molecular analyses of two mitochondrial genes.

Considering the present results of the reviewed genera and species, an illustrated key for the identification

of eastern Atlantic and Mediterranean Pisinae Dana, 1851 is provided.

## MATERIALS AND METHODS

### Morphological study

The specimens examined were accessed from several natural history and study collections: “Colección de Crustáceos Marinos del Centro Oceanográfico de Cádiz” (CRUST-IEOCD, IEO-CSIC), “Colecciones Biológicas Marinas de Referencia” (CBMR, ICM-CSIC), “Colección Zariquiey” (CBMR, ICM-CSIC), Crustacean Collection of the Naturalis Biodiversity Centre (NBC), “Museu de História Natural do Funchal” (MMF), and the private collections of J. E. García Raso, E. P. Lopes, A. M. Santos and J. A. Cuesta (all them deposited in CRUST-IEOCD). These specimens are indicated in the Results section under the respective species.

Other material examined for comparative purposes: *Anamathia rissoana*. SPAIN, Mediterranean, ♀ 36.4×27.5 mm, ICMD742/1991; Alicante, Cabo La Nao, ♂ 25.8×22.9 mm, 296–305 m, 38.49°N 0.479°E, 6 May 2003, ICMD001017. *Apiomitrax bocagei*. GUINEA-BISSAU, ♀ 27.8×26.1 mm, LANG-ABISS0211, stn 48, 63 m, 11.36°N17.09°W, 12 May 2011, IEOCD-LB0211/432-1; ♀ 33.6×31.1 mm, LANGABISS0211, stn 48, 63 m, 11.36°N17.09°W, 12 May 2011, IEOCD-LB0211/432-2; ♂ 40.6×37 mm, ♂ 39.1×34.9 mm, ♂ 31.7×31 mm, ♂ 30.2×28.1 mm, LANGABISS0211, stn 179, 26 m, 11.44°N17.07°W, 31 May 2011, IEOCD-LB0211/431. *Micropisa ovata*. CAPE VERDE, ♀ 4.8×5.0 mm, ♀ 7.4×7.5 mm, ♂ 7.0×7.3 mm, ♂ 3.5×3.8 mm, IEOCD-PISA/3039-1-2-3. *Scyramathia hertwigi*. IRELAND, Porcupine Bank, ♂ 41.1×41.1 mm, PORCUPINE13, stn 4, 492–493 m, 51.77°N 51.80°W, 5 Sep. 2013, IEOCD-PC13/1752; GUINEA-BISSAU, ovig ♀ 45.6×48.9 mm, LANGABISS0111, stn 203, 551 m, 10.01°N 17.11°W, 19 Apr. 2011, IEOCD-LB0111/404; ♂ 55×58.5 mm, BISSAU0811, stn 30, 550 m, 10.29°N 17.26°W, 28 Oct. 2008, IEOCD-GB0810/181; NAMIBIA, ♂ 29.6×32 mm, NAMIBIA0702, stn 58, 710–718 m, 27.527°S 14.51°E, 21 Feb. 2007, IEOCD-NB02/2444; ♂ 26.2×27.9 mm, NAMIBIA0702 stn 75, 502 m, 28.082°S 14.60°E, 24 Feb. 2007, IEOCD-NB02/2445.

Specimens of all species currently classified in *Pisa*, as well as individuals of *Lissa chiragra* (Fabricius, 1775), *Micropisa ovata* Stimpson, 1857 and other Pisinae were reviewed, measured and photographed. This review was undertaken after a morphological examination of the specimens and a thorough analysis of their original descriptions. The only exception was the case of *P. sanctaehelenae*, for which the morphological details were taken from the original species description. The holotype and paratypes of this species are deposited in the National Museum of Natural History

ry, Smithsonian Institution. Unfortunately, obtaining a loan of this material was not possible because of COVID-19 restrictions.

The terminology used in the descriptions and comparisons follows Davie et al. (2015) and is illustrated in Figure 1. Measurements and abbreviations used in the text and figures are: cl, maximum carapace length (without including the rostral spines as they break very easily) along the dorsal midline from the base of the rostral sinus to the posterior margin of the carapace; cw, maximum carapace width (including lateral spines) taken at its widest point, including lateral spines; G1, first gonopod; G2, second gonopod; heps, hepatic spine; intsp, intercalated spine; pol, postorbital lobe; prl, pre-orbital lobe; P2-P5, pereopods 2 to 5 (P1 is the cheliped); soe, supraorbital margin. Other abbreviations used are indet, indeterminate; juv, juvenile; ovig, ovigerous, stn, station; ♂, male; ♀, female. For *P. sanctaehelenae*, the measurements were taken from Chace (1966).

## Molecular study

Total genomic DNA was extracted from muscle tissue, eyes or eggs using a modified Chelex 10% protocol following the method described by Estoup et al. (1996). Partial sequences of the mitochondrial large ribosomal subunit (16S rRNA) and cytochrome oxidase subunit I (COI) genes were amplified through polymerase chain reaction (PCR) using the primers listed in Table 1. Owing to difficulties encountered with certain specimens, especially those from older collections, new primers were developed for the purpose of this study. Reactions were carried out using the following cycling parameters: initial denaturing at 95°C for 5 min, 35–40 cycles of 94°C for 30 sec, 40–45°C (16S rRNA), 40°C–48°C (COI) for 30 sec, 72°C for 30 sec (16S rRNA) and 45 sec (COI), and a final extension at 72°C for 5 min. Double-stranded PCR products were visualized using agarose gel electrophoresis (1% agarose) stained with GelRed® nucleic acid gel stain (Biotium), and PCR

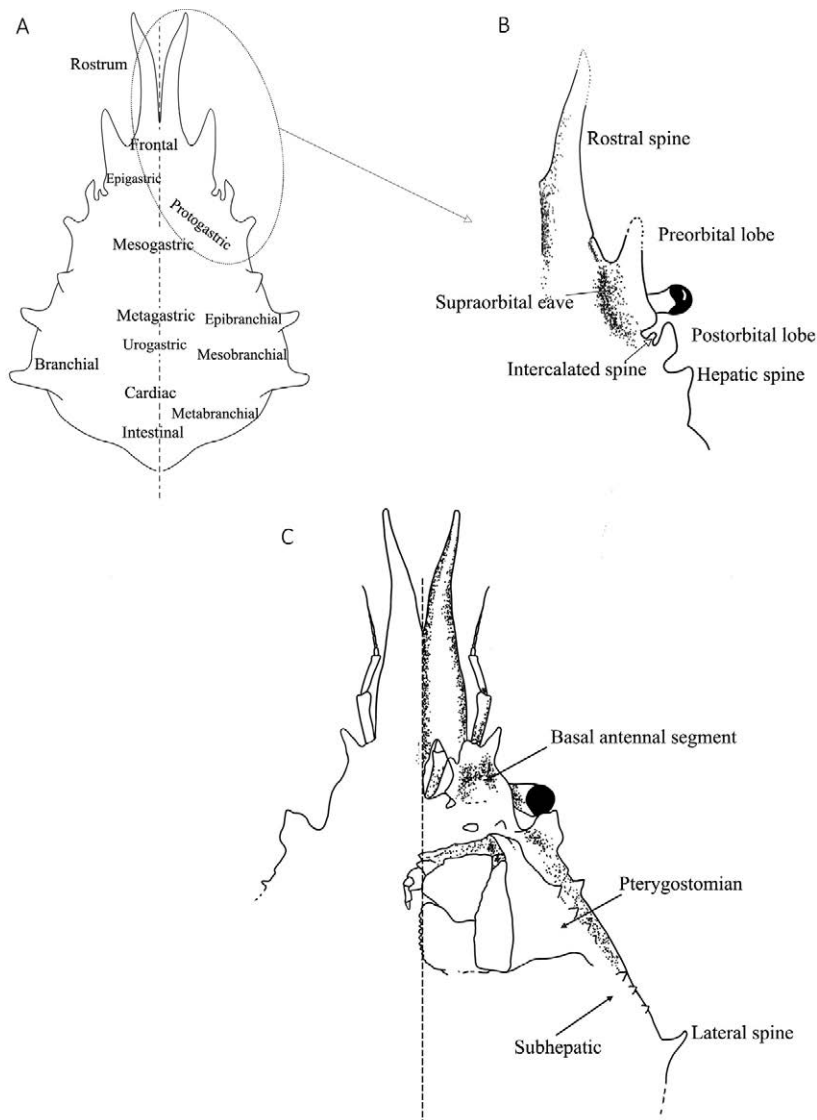


Fig. 1. – Schematic representation of an adult specimen of Pisinae. **A**, dorsal view of the carapace, **B**, details of the orbital and hepatic regions, and **C**, anteroventral view of the carapace (modified from Chace (1966) and Forest and Guinot (1966)).

Table 1. – List of sequenced genes including primers used for each gene, pair combinations, length of the sequences obtained (bp), and references.

Genes	Primers (forward and reverse)	pair	(bp)	References
16S	16SL29 (5'-YGC CTG TTT ATC AAA AAC AT-3')	1472	540	Schubart et al. (2000)
	16L12 (5'-TGA CCG TGC AAA GGT AGG ATA A-3')	1472	450	Schubart et al. (1998),
	1472 (5'-AGA TAG AAA CCA ACC TGG-3')			Crandall and Fitzpatrick (1996)
	16PISAL (5'-AAA GGT AGC RTA ATM ATT AGB-3')	1472	390	This study
	16PISAH (5'-GCT GTT ATC CCT AAA GTA ACT-3')	16MxL	390	This study
COI	COL6b (5'-ACA AAT CAT AAA GAT ATY GG-3')	COH6	670	Schubart and Huber (2006)
	COH6 (5'-TAD ACT TCD GGR TGD CCA AAR AAY CA-3')			Schubart and Huber (2006)
	LCO1490 (5'-GGTCAACAAATCATAAAGATATTG-3')	HCO2198	670	Folmer et al. (1994)
	HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3')			
	LCO1490 (5'-TNT CAN CAN AYC AYA ARG AYA TTG G-3')	Crusty_H	660	Geller et al. (2013)
		COPISAH	340	
	Crusty_H (5'-TAN ACY TCN GGR TGN CCR AAR AAY CA-3')	COPISAL	340	Varela et al. (2021)
	COPISAL (5'-TTA TCC HCC HYT NTC MGC YCG-3')			This study
	COPISAH (5'-GCR GCK GAN ARD GGD GGA TAA-3')			This study

products were sent to Stab-Vida laboratories to be purified and then bidirectionally sequenced. A manual check of misreads in the 16S rRNA and COI chromatograms was performed with the Chromas Lite software version 2.6.4 (Technelysium Pty Ltd 2017).

The sequences of 16S (576 bp) and COI (663 bp) from this study and the available COI and 16S sequences in BOLD (<http://v3.boldsystems.org/>) and GenBank (<http://www.ncbi.nlm.nih.gov>) (see Table 2) were assembled with CodonCode Aligner version 9.0 (<https://www.codoncode.com/aligner/index.htm>). *Apiomithrax violaceus* (A. Milne-Edwards, 1867) was employed as the outgroup taxon.

The translation of the COI marker was deduced using the mtDNA genetic code of invertebrates in UniPro UGENE version 1.29 (Okonechnikov et al. 2012) analyze, and visualize their data. UGENE integrates widely used bioinformatics tools within a common user interface. The toolkit supports multiple biological data formats and allows the retrieval of data from remote data sources. It provides visualization modules for biological objects such as annotated genome sequences, NGS assembly data, multiple sequence alignments, phylogenetic trees, and 3D structures. Most of the integrated algorithms are tuned for maximum performance by the usage of multithreading and special processor instructions. UGENE includes a visual environment for creating reusable workflows that can be launched on local resources or in a High Performance Computing (HPC, making it possible to verify the existence of stop codons and the presence of pseudogenes. PartitionFinder v2.1.1 (Lanfear et al. 2012) was used to determine the best-fit partitioning schemes

and models of molecular evolution for each dataset according to the Akaike information criterion (Akaike 1973). The following models of molecular evolution were applied to COI and 16S partitions: GTR+G (1st partition), TRNEF+I (2nd partition) and TVM+I (3rd partition) for COI and TVM+I+G for all 16S positions. Maximum likelihood and Bayesian inference methods were used to reconstruct *Pisa* phylogeny. For Bayesian inference analyses, performed in MrBayes v3.2.6 (Ronquist et al. 2012), the settings included five million generations, sampling every 1000 generations and discarding the first 20% of generations as burn-in. The convergence of parameter values was assessed using Tracer v1.7 (Rambaut et al. 2018), excluding an initial 10% for each run. All parameter estimates for each run showed ESS values greater than 200. A final Bayesian majority-rule consensus tree was obtained for each data set. For maximum likelihood, RAxML v8.1.16 (Stamatakis 2014) with the rapid hill-climbing algorithm and 100000 bootstrap pseudoreplicates were used. The consensus trees inferred for each method were improved using FigTree v1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>) with the maximum likelihood template as a final view.

The BEAST software version 2.2.1 (Bouckaert et al. 2014) was used to estimate a species tree by incorporating data from both genes. Burn-in was set to 5000 (corresponding to 10% of the total samples in each run) and results were checked in Tracer v1.7 to determine adequate burn-in. The convergence and ESS were also assessed with Tracer After discarding the burn-in samples. The final species tree was plotted with Tree Annotator v2.4.5 (<http://tree.bio.ed.ac.uk/software/annotator/>).

Table 2. – List of specimens used in molecular analysis, including specimen code of the institution where the DNA voucher is deposited, and accession codes of the sequences deposited in BOLD or Genbank databases. Sequences obtained in the present work in bold. (-) No sequence available.<sup>1</sup>, this COI sequence attributed to *Pisa armata* was not used because it does not belong to a *Pisa* species.<sup>2</sup>, not collection code but sample id, deposited at the “Instituto de Investigação das Pescas e do Mar” (according to BOLD), as *Pisa nodipes*.<sup>3</sup>, parental female of the larval development described by Guerao et al. (2003).<sup>4</sup>, DNA voucher identified as *Pisa hirticornis*.

Specimen id.	Specimen code	16S	COI
<i>Afropisa carinimana</i> n. comb.	MMF428227	<b>OP326676</b>	<b>OP326263</b>
<i>Afropisa carinimana</i> n. comb.	IEOCD-CCLME12/891	<b>OP326677</b>	<b>OP326264</b>
<i>Afropisa carinimana</i> n. comb.	IEOCD-GB08/182	<b>OP326678</b>	(-)
<i>Afropisa carinimana</i> n. comb.	IEOCD-PISA/3000	<b>OP326679</b>	<b>OP326265</b>
<i>Afropisa carinimana</i> n. comb.	IEOCD-PISA/3001	<b>OP326674</b>	(-)
<i>Afropisa carinimana</i> n. comb.	IEOCD-PISA/3002	<b>OP326680</b>	<b>OP326266</b>
<i>Afropisa carinimana</i> n. comb.	IEOCD-PISA/291	<b>OP326675</b>	<b>OP326262</b>
<i>Apiomithrax violaceus</i>	CCDB<BRA> 5054	MF490139	MF490070
<i>Herbstia condyliata</i>	IEOCD-PISA/293	<b>OP326683</b>	<b>OP326269</b>
<i>Micropisa ovata</i>	IEOCD-PISA/3039-2	<b>OP326681</b>	<b>OP326267</b>
<i>Micropisa ovata</i>	IEOCD-PISA/3039-3	<b>OP326682</b>	<b>OP326268</b>
<i>Pisa armata</i>	7203_LOMBOK <sup>1</sup>	(-)	OL457586
<i>Pisa armata</i>	MT04648	(-)	KT208481
<i>Pisa armata</i>	MT04649	(-)	KT208450
<i>Pisa armata</i>	ASCB110-78 <sup>2</sup>	(-)	IPID078-10
<i>Pisa armata</i>	ICMD000864	<b>OP326656</b>	(-)
<i>Pisa armata</i>	IEOCD-AR15/2551	<b>OP326653</b>	<b>OP326245</b>
<i>Pisa armata</i>	IEOCD-AR16/2552	<b>OP326654</b>	<b>OP326246</b>
<i>Pisa armata</i>	IEOCD-LANGAMAU/2181	<b>OP326655</b>	<b>OP326247</b>
<i>Pisa armata</i>	IEOCD-GE17/2133	<b>OP326652</b>	(-)
<i>Pisa armata</i>	IEOCD-PISA/3003	<b>OP326650</b>	<b>OP326243</b>
<i>Pisa armata</i>	IEOCD-PISA/3004	<b>OP326651</b>	<b>OP326244</b>
<i>Pisa armata</i>	IEOCD-PISA/292	<b>OP326649</b>	<b>OP326242</b>
<i>Pisa chiragra</i> n. comb.	ICMD297/2000 <sup>3</sup>	<b>OP326647</b>	<b>OP326240</b>
<i>Pisa chiragra</i> n. comb.	IEOCD-PISA/294	<b>OP326648</b>	<b>OP326241</b>
<i>Pisa hirticornis</i>	ICMZ2040/2016	<b>OP326672</b>	<b>OP326261</b>
<i>Pisa hirticornis</i>	ICMZ2058/2016	<b>OP326673</b>	(-)
<i>Pisa hirticornis</i>	ICMZ13887/2017	<b>OP326671</b>	<b>OP326260</b>
<i>Pisa muscosa</i>	ICMZ13865/2017	<b>OP326658</b>	(-)
<i>Pisa muscosa</i>	ICMZ2237 (o 2241)/2016	(-)	<b>OP326251</b>
<i>Pisa muscosa</i>	IEOCD-PISA/3005	<b>OP326657</b>	<b>OP326248</b>
<i>Pisa muscosa</i>	IEOCD-PISA/3006	(-)	<b>OP326249</b>
<i>Pisa muscosa</i>	IEOCD-PISA/3007	<b>OP326659</b>	<b>OP326250</b>
<i>Pisa nodipes</i>	MMF8838	<b>OP326662</b>	(-)
<i>Pisa nodipes</i>	IEOCD-PISA/3008	<b>OP326660</b>	<b>OP326252</b>
<i>Pisa nodipes</i>	IEOCD-PISA/3032	<b>OP326663</b>	<b>OP326253</b>
<i>Pisa nodipes</i>	IEOCD-PISA/3033	<b>OP326661</b>	(-)
<i>Pisa nodipes</i>	SEAMoBB_Italy_BC	(-)	ON716103
<i>Pisa tetraodon</i>	MMF23312	<b>OP326665</b>	<b>OP326254</b>
<i>Pisa tetraodon</i>	ULLZ11427	KF452980	KF452902
<i>Pisa tetraodon</i>	UB2011PH <sup>4</sup>	KC866332	(-)
<i>Pisa tetraodon</i>	IEOCD-PISA/3010	<b>OP326666</b>	<b>OP326255</b>
<i>Pisa tetraodon</i>	IEOCF-PISA/3012	<b>OP326664</b>	(-)
<i>Pisa tetraodon</i>	IEOCD-PISA/3014	<b>OP326667</b>	<b>OP326256</b>
<i>Pisa tetraodon</i>	IEOCD-PISA/3016	<b>OP326668</b>	<b>OP326257</b>
<i>Pisa tetraodon</i>	IEOCD-PISA/3037	<b>OP326669</b>	<b>OP326258</b>
<i>Pisa tetraodon</i>	IEOCD-PISA/3038	<b>OP326670</b>	<b>OP326259</b>
<i>Samadinia galathea</i>	IEOCD-MZ09/1802-1	MZ424947	MZ434792
<i>Samadinia pulchra</i>	IEOCD-MZ08/1819-2	MZ424950	MZ434795

Consensus trees were visualized in FigTree and later modifications, such as the insertion of later values and colouring of branches, were performed with Inkscape version 0.48 (<http://www.inkscape.org>).

**Molecular data**

Few published studies include DNA sequences of *Pisa* species. Windsor and Felder (2014) provided sequences for the 12S, 16S, 18S and COI genes for a

single specimen of *P. tetraodon*. Raupach et al. (2015) gave two different COI sequences for *P. armata*, and Mugnai et al. (2023) provided two identical COI sequences for *P. nodipes*, although one is submitted under the name of *P. armata*. Additionally, there is a short (~400 bp) COI fragment submitted by Fernandez (unpublished) for *P. tetraodon*, and another COI sequence attributed to *P. armata* from Lombok Island (Indonesia) deposited by Ambariyanto et al. (unpublished). The latter identification is likely to be wrong, since its average genetic distance from other *Pisa* species,

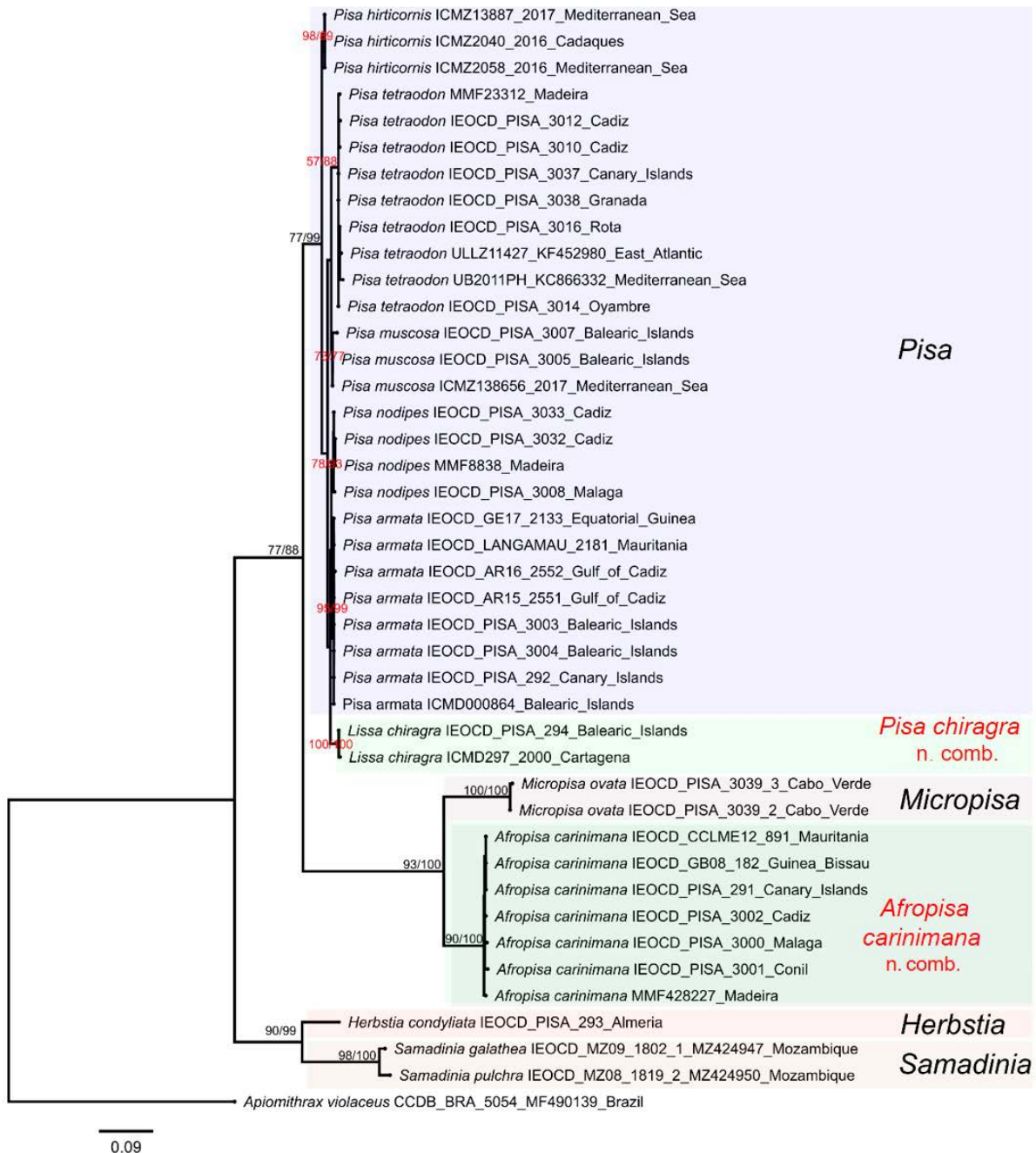


Fig. 2. – Phylogenetic relationships of Epialtidae species inferred from the combined maximum likelihood and Bayesian analysis of 16S rRNA. Tree topology was obtained from maximum likelihood analysis. Scale bar represents 0.09 substitutions per site. The bootstrap values for maximum likelihood and Bayesian analysis appear one after the other at each node, respectively. *Apiomithrax violaceus* sequence was used as outgroup.

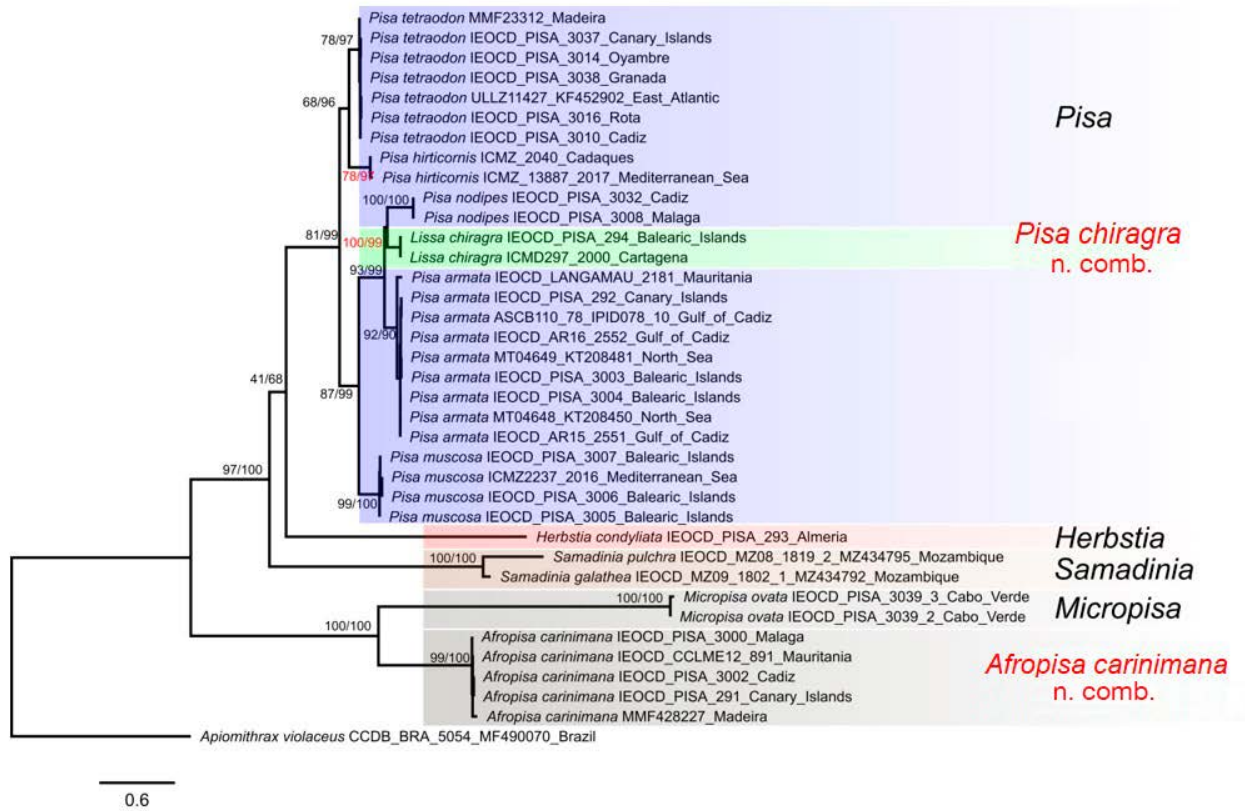


Fig. 3. – Phylogenetic relationships of Epialtidae species inferred from the combined maximum likelihood and Bayesian analysis of COI. Tree topology was obtained from maximum likelihood analysis. Scale bar represents 0.09 substitutions per site. The bootstrap values for maximum likelihood and Bayesian analysis appear one after the other at each node, respectively. *Apiomithrax violaceus* sequence was used as outgroup.

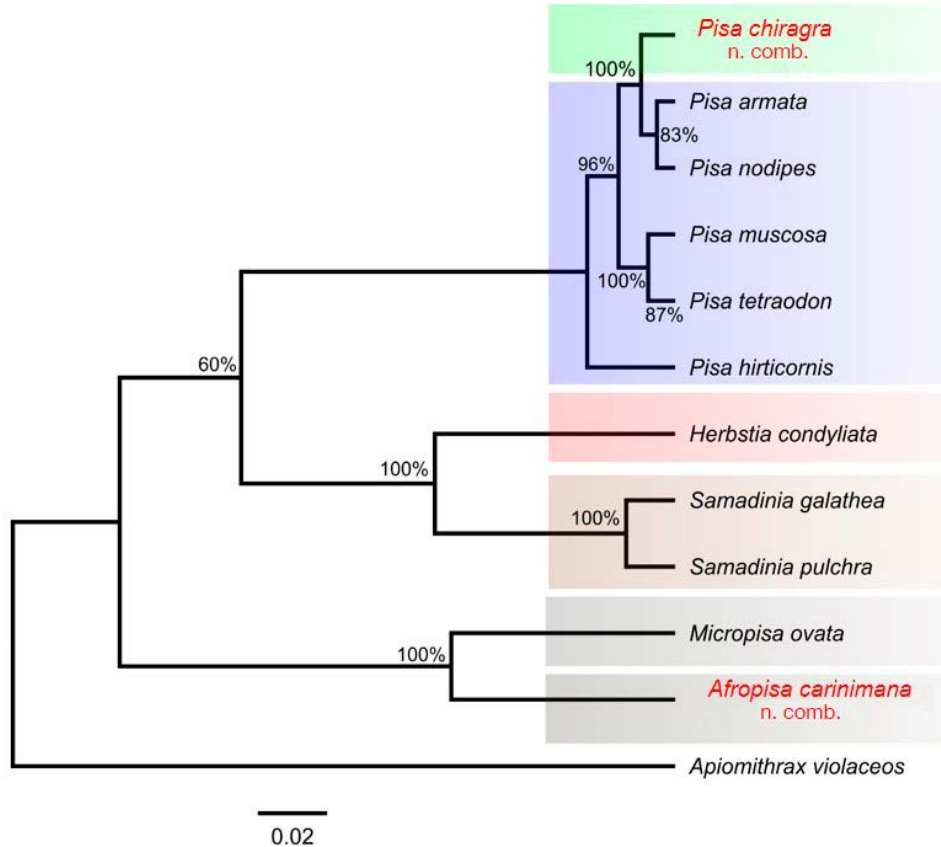


Fig. 4. – Epialtidae species tree estimated according to a fully Bayesian multispecies coalescent method implemented in StarBEAST2 based on mitochondrial COI and 16S rRNA markers. *Apiomithrax violaceus* sequence was used as an outgroup.

is at least 11.5%. In BOLD, excluding the sequences mined from GenBank, there is one COI sequence for *P. armata* (identified as *P. nodipes*) from the Algarve (Portugal) and nine COI sequences of *P. carinimana* marked as “early-release” and therefore not available for use in this study. DNA barcodes were obtained from nine species with a total of 37 and 30 new 16S and COI sequences, respectively, (see Table 2) in the present study.

Molecular data obtained and analysed in the present study support the species composition of the genus *Pisa*, including *P. hirticornis* (see Figs 2–4); *Pisa* is a monophyletic group when it includes *Lissa chiragra* (as *Pisa chiragra* n. comb. in Figs 2–4) and when *P. carinimana* (as *Afropisa carinimana* n. comb. in Figs 2–4) is placed in a new genus. From this point forward, these changes will be implemented for the mentioned species.

Two distinct groups can be observed within *Pisa*, and this grouping is also supported by morphological evidence. One group includes *P. armata*, *P. nodipes* and *P. chiragra* n. comb., while the other group consists of *P. muscosa*, *P. hirticornis* and *P. tetraodon*. Furthermore, *Afropisa carinimana* n. comb. is phylogenetically closer to *Micropisa* Stimpson, 1857 than to *Pisa* (Figs 2–4).

## Morphological examination

The morphological study further supports the proposal to establish a new genus for *P. carinimana* (which is also supported by molecular data, as mentioned earlier), as well as for *P. sanctaehelenae* and *P. calva*, separate from the other species within *Pisa*.

## SYSTEMATIC ACCOUNT

Family Epialtidae MacLeay, 1838  
Subfamily Pisinae Dana, 1851  
Genus *Afropisa* n. gen.

**Diagnosis** (Figs 5G–I, 6G–H). Carapace subpyriform, longer than wide, with regions well delimited. Rostral spines divergent from the base or close to it, in V-shape or U-shape. Orbital margin: supraorbital margin projected forward in a protruding angular lobe, intercalated spine or tooth between supraorbital margin and postocular process; flat plate-shaped postocular process (dorsal view). A strong spine on hepatic region behind postocular process. Laterobranchial margins with one to four spines. Basal antennal segment with distal outer spine visible from above (between the rostral spines and the supraorbital margin), and a distinct tooth or elongated bump just posterior to posterolateral angle of antennal basal segment.

Pterygostomial region with three or four tubercles along the lateral margin, decreasing in size posteriorly (Fig. 7A1).

Mesogastric region bulging and prominent, with one small anterior tubercle; cardiac region highly convex or swollen surrounded by a deep furrow, both without spines.

Intestinal region with a median prominence, small spine or tubercle. Dorsal branchial regions with protuberances on each side: one or two small blunt epibranchial tubercles and one mesobranchial blunt spine or lobe.

Cheliped: merus with prominent tubercles on dorsal midline, with one large tubercle on the dorsal articulation with the carpus; propodus with well-defined ventral margin (resembling a keeled structure).

Male G1 slender, rather straight proximally, slightly curved subdistally, with broadened distal part. The outer distal side is pointed and shows a subdistal small finger-like process projecting inward (sometimes not visible), and the inner distal side is like a downward- or upward-curved projection or tongue (Fig. 7B, Forest and Guinot 1966: Figs 12–13; Chace 1966: Fig. 14g, h).

Specimens of relatively small sizes.

**Type species.** *Pisa carinimana* Miers, 1879, by present designation. Topotypic locality: Canary Islands. Holotype deposited in British Museum (according to Monod 1956).

**Other species included.** *P. sanctaehelenae* Chace, 1966 and *P. calva* Forest and Guinot, 1966.

**Material examined.** See below under the respective species within this new genus.

**Etymology.** The root “Afro” means African or native to Africa, referring to the main localities of the species within the new genus, and the ending “pisa” refers to the genus *Pisa*, where these species were originally classified. The genus name is feminine.

**Remarks.** *Afropisa* n. gen. mainly differs from *Pisa* by having a small and subpyriform carapace; rostral spines divergent from the base or close to it, in V-shape or U-shape (Figs 5G–I, 6G–H); pterygostomial region with three or four tubercles along the lateral margin, decreasing in size posteriorly (however, in some specimens of *A. carinimana* n. comb. only a pair of tubercles can be found in one of the pterygostomial areas) (Fig. 7A1); and male G1 with a small finger-like process projecting inward on the outer distal plate that is absent in the *Pisa* species (Figs 7B, 8A–E; Zariquiey Álvarez 1968, Figs 154 a–e, 156c), which tend to have a more prominent, upward-directed external distal plate.

*Micropisa* can be easily differentiated from *Afropisa* n. gen., as well as from *Pisa* by the absence of the intercalated spine or lobe on the orbital margin (A. Milne-Edwards 1868: pl. 16, Fig. 1; Monod 1956: Fig. 669). However, *Micropisa* shares the morphology of the male G1 with *Afropisa* n. gen. because of a small finger-like process projecting inward on the outer distal lobe (Monod 1956: Figs 679–681). In addition, Monod (1956: 499), when comparing *Micropisa* with *Pisa*, mentioned that Stimpson (1857) stated that “there was a generic difference also in the *mcp* 3, whose merus would be without a notch for the reception of the carpus in *Micropisa* and with a notch in *Pisa* (Figs 7A2,3); however, *P. carinimana* (which cannot be separated from the other *Pisa*) has no notch” (Fig. 7A1).



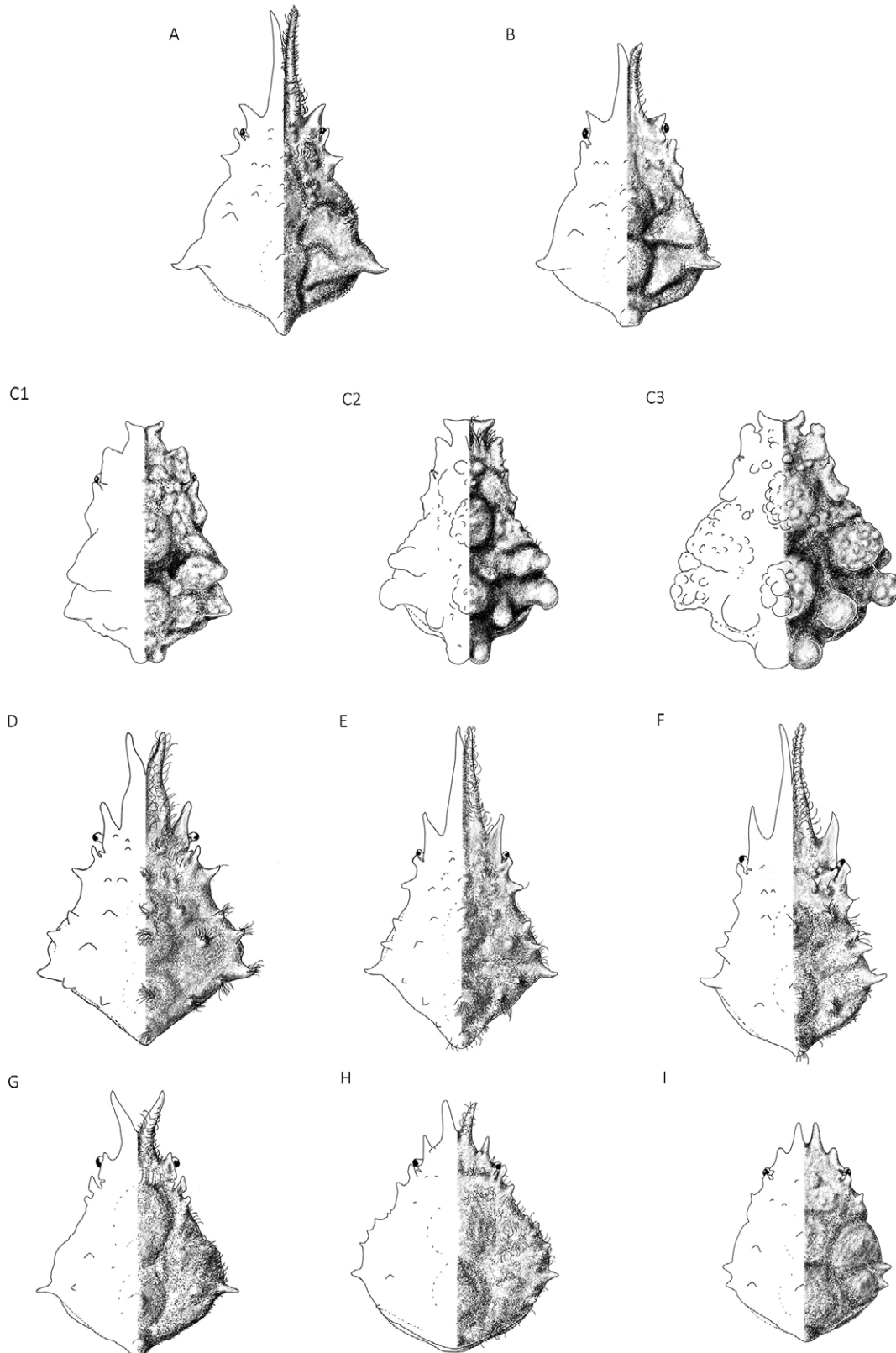


Fig. 5. – Scheme of adult specimens of *Pisa* and *Afropisa* n. gen. species. **A**, *Pisa armata* ♂ 29×31.2 mm, from Guinea-Bissau; **B**, *Pisa nodipes* ♂ 17.7×21.9 mm, from Funchal, Portugal; **C**, *Pisa chiragra* n. comb. (1) juv ♀ 10.1×13.5 mm, from Balearic Islands, Spain (2) ♀ 20×27 mm, from Balearic Islands, Spain; (3) ovigerous ♀ 31.9×32.4 mm, from Murcia, Spain; **D**, *Pisa tetraodon* ♂ (25.1×28 mm, from Cádiz, Spain); **E**, *Pisa hirticornis* ♂ 25.2×27.3 mm, from Girona, Spain; **F**, *Pisa muscosa* ♂ 13.2×14.9 mm from Girona, Spain; **G**, *Afropisa carinimana* n. comb. ♂ 10.9×12 mm, from Mauritania; **H**, *Afropisa sanctaehelena* n. comb. ♂ (based on Chace 1966); **I**, *Afropisa calva* n. comb. ♀ 7.6×8.4 mm, from Equatorial Guinea.

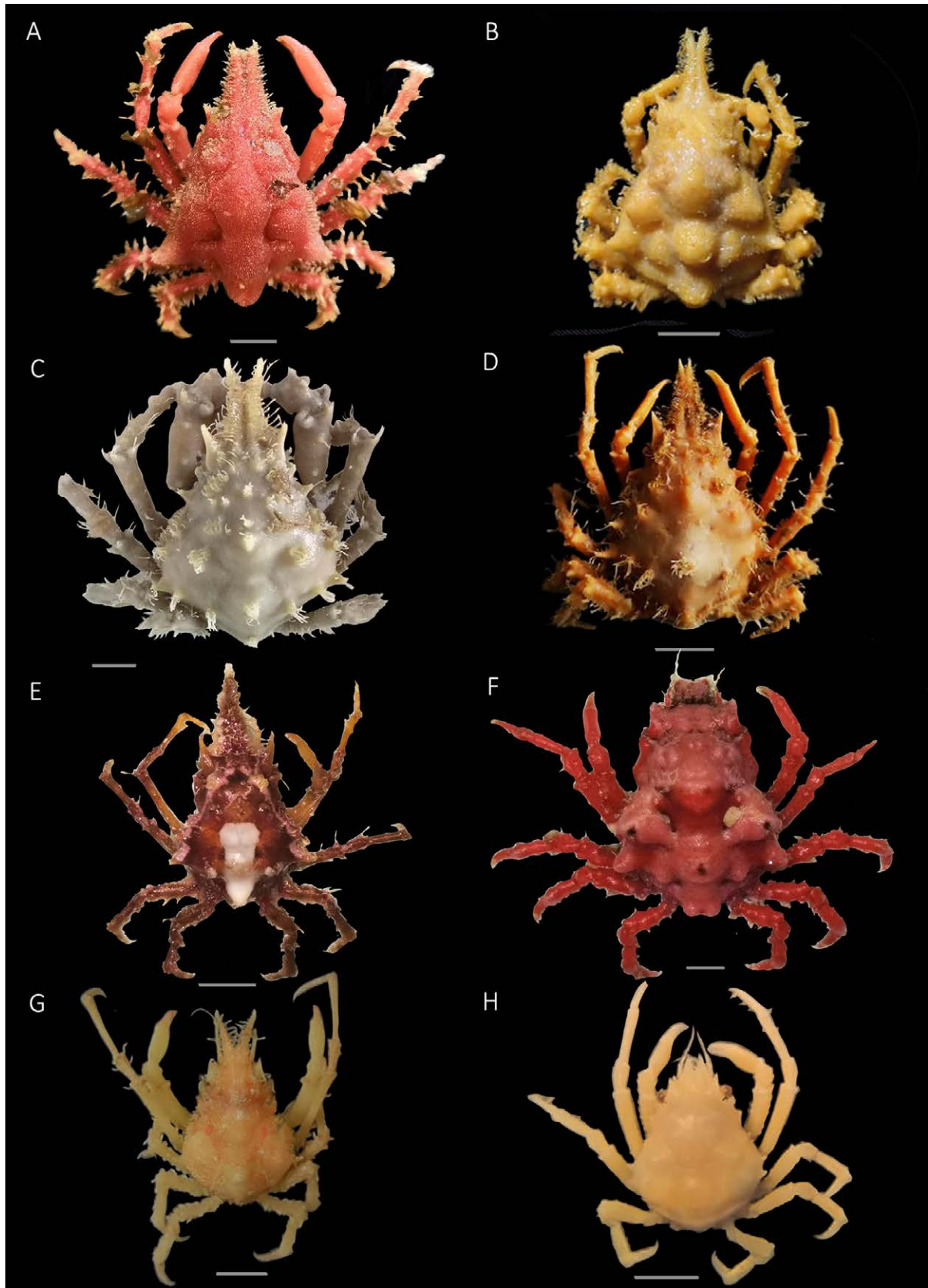


Fig. 6. – Dorsal habitus of the species of *Pisa* and *Afropisa* n. gen. **A**, *Pisa armata* (Latreille, 1803), ♂ IEO-CD-GB08/180; **B**, *Pisa nodipes* (Leach, 1815), ♀ MMF 15797 (preserved); **C**, *Pisa tetraodon* (Pennant, 1777), ♂ IEOCD-PISA/3012 (preserved); **D**, *Pisa hirticornis* (Herbst, 1804), ♀ ICMZ2070/2016; **E**, *Pisa muscosa* (Linnaeus, 1758), ♂ IEOCD-MÉDITS22/301; **F**, *Pisa chiragra* (Fabricius, 1775) n. comb., juv ♀ IEOCD-MÉDITS22/300; **G**, *Afropisa carinimana* (Miers, 1879) n. comb. ♂ IEOCD-CCLME12/1175; **H**, *Afropisa calva* (Forest and Guinot 1966) n. comb. ♀ RMNH.CRUS.D.23910 (preserved). Scale bars: 0.5 cm.

***Afropisa carinimana* (Miers, 1879)**  
n. comb. (Figs 5G, 6G, 7A1, B)

*Pisa carinimana* Miers, 1879: 11–12 (superseded combination).

**Material examined.** Portugal, Madeira, Bay of Funchal, ovig ♀ 5.3×5.6 mm, 28 Nov. 2013, MMF 42827. Spain, Canary Islands, Gran Canaria, Maspalomas, ovig ♀ 5.3×7.1 mm (cw × cl), ♀ 5.8×7.2 mm, CIRCAN2020, stn 21, 65–70 m, 27.71°N 15.55°W, 27 Nov. 2020, IEOCD-CIRCAN20/3017; Canary Islands, Lanzarote, La Lajita, ♀ 3.4×4.2 mm, ovig ♀ 4.9×5.7 mm, 2 ♂ 5×6.1 mm, 2.7×3.5 mm, CIRCAN2020, stn 55, 53–54 m, 28.15°N 14.16°W, 2 Dec. 2020, IEOCD-CIRCAN20/3018; Canary Islands, Fuerteventura, 9 Jul. 2012, IEOCD-PISA/291 (damaged); Málaga, Caleta de Vélez, ♂ 15.65×15.97 mm, 24–26 m, 36.74°N 4.071°W, 31 May 1978, IEOCD-PISA/3019; Málaga, Caleta de Vélez, ♂ 10.97×12.58 mm, ♂ 15.48×15.65 mm, ♀ 10.1×10.48 mm, 36.74°N 4.071°W, 1 Aug. 1979, IEOCD-PISA/3022; Málaga, Fuengirola, ♀ 10.08×12.42 mm, ♀ 12.74×12.26 mm, 26–31 m, 36.53°N 4.61°W, 14 Jul. 1976, IEOCD-PISA/3020; Málaga, Marbella, ♂ 9.03×10.81 mm, 33–44 m, 36.49°N 4.88°W, 21 Dec. 1978, IEOCD-PISA/3021; Málaga, Calahonda, ♀ 10.32×10.97 mm, ♂ 5.6×6.5 mm, 1–5 m, 36.69°N 3.41°W, 9 Feb. 2005, IEOCD-PISA/3023; Málaga, Calaburras-Cabo Pino, ♂ 12.7×13.06 mm, 15 m, 36.50°N 4.63°W, 18 May 2005, IEOCD-PISA/3024; Málaga, Calaburras, ♂ 12.74×13.2 mm, ♀ 8.55×10.32 mm, infralittoral, 36.50°N 4.63°W, Aug. 1991, IEOCD-PISA/3028; Málaga, Cabo Pino, ♂ 11.2×12.5 mm, 22 m, 36.50°N 4.63°W, Sept. 2004, IEOCD-PISA/3000; Granada, La Herradura, ovig ♀ 11.61×13.06 mm, 3.4 m, 36.72°N 3.75°W, Jun. 2020, IEOCD-PISA/3025; Granada, La Herradura, Marina del Este, ♂ 10.32×10.97 mm, 2–3 m, 36.72°N 3.75°W, 4 Mar. 2018, IEOCD-PISA/3026; Granada, La Herradura, ovig ♀ 15.32×15.48 mm, ovig ♀ 4.7×5.6 mm, infralittoral, 36.72°N 3.75°W, Aug. 1991, IEOCD-PISA/3027; Cádiz, La Caleta, ♂ 8.1×8.4 mm, intertidal, 36.53°N 6.31°W, 28 Oct. 2015, IEOCD-PISA/3002; Cádiz, Conil, ♂ 8.9×10.6 mm, 36.27°N 6.09°W, 14 Jul. 2015, IEOCD-PISA/3001. Morocco, ♂ 15.5×16.6 mm, 56 m, 30 Jun. 2012, CCLME2012, stn 234, 28.25°N 12.54°W, IEOCD-CCLME12/1205. Western Sahara, ♂ 17.6×17.2 mm, CCLME2012, stn 202, 68 m, 25.11°N 15.45°W, 19 Jun. 2012, IEOCD-CCLME12/1178; indet specimen (damaged), 109–110 m, CCLME2012, stn 286, 25.50°N 15.69°W, 20 Jun. 2012, IEOCD-CCLME12/1156. Mauritania, ♀ 7.9×9 mm, ♂ 10.9×12 mm, CCLME2012, stn 145, 30 m, 19.31°N 16.74°W, 8 Jun. 2012, IEOCD-CCLME12/891. Guinea-Bissau, ♂ 7.2×10.3 mm, BISSAU0811, stn 87, 38 m, 10.53°N 16.43°W, 8 Nov. 2011, IEOCD-GB08/182.

**Size.** Relatively small size: cl (without rostral spines) 15.97 mm in males, and 15.48 mm in females; ovigerous females from 13.06 mm cl.

**Description.** Specimens morphologically agree well with descriptions by Miers (1879: 11, pl. IV, Fig. 6), Monod (1956: 488–495, Figs 655–668), Forest and Guinot (1966: 99–103, Figs 12a, b) and Zariquiey Álvarez (1968: 453–454, Fig. 155a).

**Distribution.** Eastern Atlantic: from Spain to Angola (Forest and Guinot 1966, d’Udekem d’Acoz 1999, Marco-Herrero et al. 2015), including Madeira (Ramalhosa et al. 2014) and the Canary Islands (González 2018). Mediterranean: Alboran Sea (Málaga, Granada and Almería) (Zariquiey Álvarez 1968, García Raso 1990, García Raso et al. 2006).

**Habitat.** On shell bottoms, gravel bottoms (Fransen 1991), sandy bottoms with algae (García Raso 1984), sand and muddy sand bottoms, muddy bottoms often with bryozoa or foraminifera; occasionally on hard substrates (Manning and Holthuis 1981). Between 4 (Capart 1951) and 110 m depth (present work).

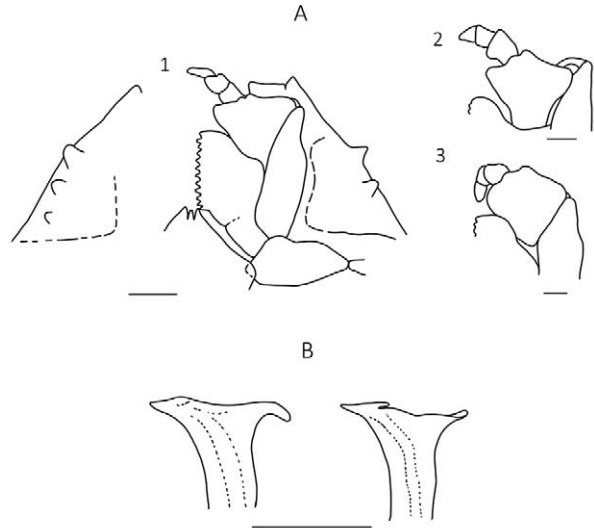


Fig. 7. – *Afropisa carinimana* n. comb., **A1**, pterygostomian regions and detail of the right third maxilliped, in ventral view; **B**, distal part of the first male left gonopods in two specimens from Cabopino-Calahonda (Málaga, Spain). **A2**, *Pisa armata*, details of merus of third left maxilliped. **A3**, *Pisa chiragra* n. comb., detail of merus of left third maxilliped. Scale bars: A1, 2, 3 = 1 mm; B = 0.5 mm.

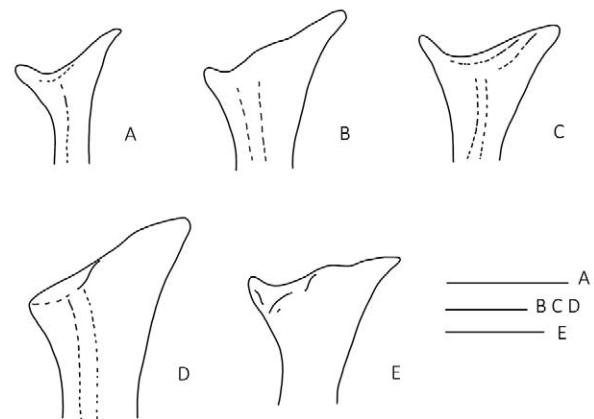


Fig. 8. – Distal part of first male gonopod of *Pisa* species. **A**, *P. muscosa*, **B**, *P. nodipes*; **C**, *P. armata*; **D**, *P. chiragra* n. comb.; **E**, *P. tetraodon*. All specimens from Málaga, Spain (coll. García Raso). Scale bars: 0.5 mm.

**Remarks.** *Afropisa carinimana* (Miers, 1879) n. comb., as the type species of the new genus *Afropisa* n. gen., matches the general characters described above for *Afropisa* n. gen. It is a small species with a subpyriform carapace; rostral spines in V-shape and divergent from the base or close to it (Figs 5G, 6G); a row of three prominent tubercles tapering posteriorly on each pterygostomian region (Fig. 7A1); and male G1 with a small finger-like process projecting inward on the outer distal plate (Fig. 7B). Additionally, *A. carinimana* n. comb. does not have a well-differentiated lobe in the merus of the third maxilliped at the level of the carpal insertion (Fig. 7A1, Monod 1956: Figs 658–661), as does *Pisa* (Figs 7A2, 7A3).

Both morphological characteristics and the results of molecular analyses support the establishment of a new genus for *P. carinimana*, which has turned out to be closer to *Micropisa* than *Pisa*.

***Afropisa sanctaehelenae*** (Chace, 1966)  
n. comb. (Fig. 5H)

*Pisa sanctaehelenae* Chace, 1966: 651–654, Figs 14a–h (superseded combination).

*Material examined.* It was not possible to obtain specimens for the reasons mentioned in the Material and Methods section. Thus, the only information available is that mentioned in the original description by Chace (1966).

*Size.* *A. sanctaehelenae* n. comb. reaches 11.3 mm in cl (including rostral spines) in males, 8.2 mm in females, and from 5.8 mm cl in ovigerous females (Chace 1966).

*Description.* See Chace (1966).

*Distribution.* Eastern Atlantic: only known from its type locality, St. Helena Island, off Rupert's Bay (Chace 1966).

*Habitat.* Collected from a buoy and cable at that location, 0–2 m depth (Chace 1966).

*Remarks.* According to the description and figures (Chace 1966, Forest and Guinot 1966), *P. sanctaehelenae* exhibits similar morphological characteristics to *A. carinimana* n. comb., such as a subpyriform carapace (not including rostral and lateral spines) that is from one-sixth to one-third longer than wide (Chace 1966, Forest and Guinot 1966), similar in size and relatively small. Both species bear three spines in the pterygostomial area vs one spine in *Pisa*. G1 of males are also similar (Chace 1966, Figs 14h–g, Forest and Guinot 1966, Figs 12a–b), but different from those of *Pisa* (Zariquiey Alvarez 1968, Figs 154 a–e, 156c).

Since DNA sequences from *P. sanctaehelenae* were not available for inclusion in the molecular analyses, its placement within *Afropisa* n. gen. could not be determined based on genetic data. However, considering its morphology, *P. sanctaehelenae* appears to be consistent with the characteristics of *Afropisa* n. gen. and could potentially be included within this new genus.

***Afropisa calva*** (Forest and Guinot, 1966)  
n. comb. (Figs 5I, 6H)

*Pisa calva* Forest and Guinot, 1966: 99–104, Figs 10–13 (superseded combination).

*Material examined.* Equatorial Guinea, Annobon, ♂ 6.0×6.8 mm (cw x cl), ovig ♀ 6.5×7.5 mm, ovig ♀ 6.7×7.3 mm, ♂ 2.1×2.7 mm, ♂ 4.1×4.8 mm, ♂ 4.1×4.5 mm, ♀ 7.6×8.4 mm, ovig ♀ 5.5×6.4 mm, PILLSBURY, stn 282, 18 m, 18 May 1965, RMNH. CRUS.D.23910.

*Size.* *A. calva* n. comb. is a small species; cl (including rostral spines) is 14 mm for males and 10.5 mm for females (Forest and Guinot 1966).

*Description.* See Forest and Guinot (1966).

*Distribution.* Eastern Atlantic: São Tomé and Príncipe, and Annobon, Equatorial Guinea (Forest and Guinot 1966).

*Habitat.* Mainly on calcareous algae bottoms, but also on sand and mud substrates, up to 73 m depth (Forest and Guinot 1966).

*Remarks.* Despite the inability to obtain DNA from the tissue samples of the specimens loaned by the Naturalis Biodiversity Centre (RMNH. CRUS.D.23910), the morphological characteristics of this species differentiate it from *Pisa* and suggest a closer affinity to *Afropisa* n. gen.

The carapace regions in this species are distinguishable, but they are less pronounced than in *Pisa*. The prominences or tubercles, such as the cardiac, gastric and branchial ones, are less developed and do not possess sharp spines and a surrounding deep furrow as in *Pisa*. However, a residual intestinal furrow is present. *Afropisa calva* n. comb. can be differentiated by several characteristics. One notable feature is the presence of up to four spines in the sub-hepatic region, which are smaller in size than the lateral spines. This distinguishes *Afropisa calva* from other related species. Sparsely hairy carapace, but with clubs of hooked setae in rostral and lateral regions of carapace (Forest and Guinot 1966). Rostrum short, U-shaped rostral spines (slightly divergent) tapered towards the end and reaching the end of the antennular peduncles, but without going beyond them. *Afropisa calva* n. comb. exhibits a basal antennal segment with an anterior spine that is slightly visible from above. Additionally, it has an elongated tooth located just posterior to the posterolateral angle of the basal antennal segment, similar to that of *A. carinimana* n. comb., which is distinctly different from the tubercle-shape tooth observed in *Pisa* species. These characteristics serve as distinguishing features for *Afropisa calva*.

Although *A. calva* n. comb., *A. carinimana* n. comb. and *A. sanctaehelenae* n. comb. are closely related (as indicated in the genus diagnosis above), they can be easily differentiated based on the following key characteristics: *A. calva* n. comb. has a shorter rostrum which is divergent from its base with a U-shape vs a longer rostrum with rostral spines joined from their base that diverge sharply in *A. carinimana* n. comb. and *A. sanctaehelenae* n. comb. *Afropisa calva* n. comb. has two subequal laterobranchial spines vs one in *A. carinimana* n. comb. and four in *A. sanctaehelenae* n. comb.

Additionally, in comparison with other species of *Pisa* and even *Afropisa* n. gen., *A. calva* n. comb. exhibits a more rounded carapace (not including

rostral and lateral spines). The length of the carapace is slightly greater than its width, with a ratio ranging from 1.08 to 1.16 for adult females and from 1.09 to 1.17 times for adult males, as determined from our measurements. The authors did not consider these proportions in young males. Forest and Guinot (1966) mentioned the ratio as being between 0.9 and 1.3 times. Its carapace is even slightly more rounded than that of *A. carinimana* n. comb.

### Genus *Pisa* Leach, 1814

*Arctopsis* Lamarck, 1801 (name suppressed).  
*Blastus* Leach, 1814 (junior subjective synonym).  
*Blastia* Leach in White, 1847 (incorrect spelling of junior synonym).  
*Lissa* Leach, 1815: 69–70 (junior subjective synonym).

*Type species:* *Pisa armata* (Latreille, 1803). Topotypic locality: Mediterranean.

*Material examined.* See on each species.

*Modified diagnosis* (Figs 5A–F, 6A–F). Carapace triangular, longer than wide. Frontal region produced as a relatively long bifid rostrum, welded at the base and diverging distally. Supraorbital margin projected forward in a protruding pre-orbital angular lobe or spine, intercalary spine present between supraorbital margin and postorbital process. Postorbital process flat plate-shaped (in dorsal view); less in *P. chiragra* which is lobulated (until now included in the monospecific genus *Lissa*). Behind postocular process, a hepatic spine with different development, from well developed to reduced or absent. Laterobranchial margins with lobes and/or spines, depending on the species.

The basal antennal segment has a tubercle-shaped tooth in the lower-outer margin. Pterygostomial region with a pair of tubercles.

Dorsal regions well defined, which can be protruding with blunt or spiniform tubercles of different shapes and developments. With protogastric tubercles well defined, central gastric region bulging and prominent, in front of which there is a small tubercle; cardiac region highly convex or swollen surrounded by a deep furrow, both not spiniform. Dorsal branchial regions with tubercles: one or two small blunt epibranchial tubercles and a blunt or somewhat projecting mesobranchial lobe. Intestinal region with median prominence, small spine or tubercle.

G1 of male slender, rather straight proximally and slightly curved subdistally, with the distal part widened and with its outer and inner lateral margins protruding upwards; the outer one is larger, wider, and more protruding than the inner one (Figs 8A–E) (Figs 154 a–e, Zariquiey Álvarez 1968).

*Remarks.* Lamarck (1801) established *Arctopsis* in a rather vague manner (withouth specifying the capture location), while *Pisa* was well described and had been used for many years. Afterward, *Arctopsis* was mentioned by Gray (1850) in his list of crab specimens in the British Museum, and he considered *Cancer biaculeatus* Montagu, 1813, *P. biaculeata* Leach, 1814 and *P. gibb-*

*sii* Leach, 1815 as synonyms of this species. Moreover, Gray (1850) also synonymized *Arctopsis tetraodon* with *P. tetraodon*. White (1857: 14, 21), in his list of crustacean specimens in the Collection of the British Museum (mainly based on the same material already listed by Gray 1850), added two records of *A. lanata* from the Isle of Man and Guernsey, and illustrated the species. His figure closely resembles *P. armata*. Apart from White (1857), no one else has recorded this species since its description.

Holthuis (1962) dealt with the issue of *Arctopsis* Lamarck, 1801 and *A. lanata* and used the diagnosis of the synonymous *Pisa* instead of *Arctopsis*, considering this as a *nomen dubium*. Consequently, the name *Arctopsis* was suppressed according to the Law of Priority but not the Law of Homonymy (China 1964: 208–209, Opinion 708, ICZN), and *P. armata* became the type species of *Pisa*.

According to our molecular and morphological data, the genus *Pisa* should be restricted to *P. armata*, *P. chiragra* n. comb., *P. hirticornis*, *P. muscosa*, *P. nodipes* and *P. tetraodon*.

### *Pisa armata* (Latreille, 1803) (Figs 5A, 6A)

*Arctopsis lanata* Lamarck, 1801 (name suppressed); White 1847: 6 (list); White 1857: 21, pl. 1 Fig. 2; Holthuis 1962c: 184 (discussion); China 1964: 208 (name suppressed under the plenary powers).

*Maia armata* Latreille, 1803 (superseded combination); China 1964: 208 (placed on the Official List of Specific Names in Zoology, name No. 1987).

*Cancer biaculeatus* Montagu, 1813 (junior subjective synonym).

*Pisa gibbsii* Leach, 1816 (junior subjective synonym).

*Blastia tridens* Leach in White, 1847 (not available name, ICZN Article 11.6).

*Material examined.* Portugal, Azores, ovig ♀, 23.9×26.0 mm, MMF 23698. Spain, Cádiz, ♂ 23.5×31 mm, ARSA1115 stn 43, 36.01°N 6.44°W, Nov. 2015, IEOCD-AR15/2551; Cádiz, ♂ 9.5×14 mm, ♂ 9.8×11.6 mm, ARSA1116 stn 37, 36.01°N 6.44°W, Nov. 2016, IEOCD-AR16/2552; Canary Islands, ♀ 12.3×13.3 mm, CIRCANA2020 stn 37, 70 m, 27.80°N 15.82°W, 29 Nov. 2020, IEOCD-CIRCANA20/3015; Menorca, Maó, ♀ damaged, 72 m, 39.82°N 4.37°E, 29 Jan. 2014, ICMD000864; Menorca, Maó, ♂ 8×10 mm, MAO14 stn 129, 39.82°N 4.37°E, 1 May 2015, IEOCD-PISA/3003; Menorca, Maó, ♂ 9.2×10.6 mm, MAO14 stn 7, 39.82°N 4.37°E, 16 May 2015, IEOCD-PISA/3004; Canary Islands, Fuerteventura, 9 Jul. 2010, IEOCD-PISA/292. Western Sahara, indet 15.1×15.6 mm, CCLME12, stn 157, 206 m, 25.52°N 15.67°W, 20 Jun. 2012, IEOCD-CCLME12/1156; damaged, CCLME11 stn 171, 113 m, 22.63°N 17.46°W, 21 Nov. 2011, IEO-CD-CCLME11/958; ovig ♀ 21.5×22.0 mm, ♂ 23.8×23.5 mm, CCLME12 stn 106, 179 m, 22.68°N 17.18°W, 14 Jun. 2012, IEO-CD-CCLME12/1152. Mauritania, ♂ 27.1×28.5 mm, LANGAMAU0114 stn 1, 275 m, 18.88°N 16.78°W, 22 Mar. 2014, IEOCD-LANGAMAU/2181; ♀ 18.8×20.4 mm, CCLME11 stn 112, 169 m, 17.09°N 16.96°W, 20 Nov. 2011, IEOCD-CCLME11/1959. Guinea-Bissau, ♀ 27.7×27.8 mm, ♂ 24.6×25.3 mm, BISSAU0811 stn 5, 102–105 m, 11.48°N 17.19°W, 23 Oct. 2008, IEOCD-GB08/179; ♂ 29.0×31.3 mm, BISSAU0811 stn 69, 65–70 m, 10.28°N 16.37°W, 4 Nov. 2008, IEOCD-GB08/180; ♂ 29×31.2 mm, BISSAU0811 stn 69, 65–70 m, 10.28°N 16.37°W, 4 Nov. 2008, IEOCD-GB08/180. Guinea, ♂ 27.2×28.9 mm, CCLME12, stn 2, 94 m, 8.95°N 14.62°W, 10 May 2012, IEOCD-CCLME12/1594. Sierra Leone, ♀ 24.1×26 mm, GUINEA90 stn 71, 55–60 m, 7.25°N 13.20°W, 13 Apr. 1990, IEOCD-PISA/3030. Liberia, ♂ 35.1×38 mm, GUINEA90 stn 35, 44–47 m, 5.44°N 10.04°W, 6 Apr. 1990, IEOCD-PISA/3031. Equatorial Guinea, Bioko, ♀ 27.8×29 mm, GECUAT0817 stn 7, 63 m, 3.67°N 8.98°E, 8 Aug. 2017, IEOCD-GE17/2133.

**Distribution.** Eastern Atlantic: from British Isles and south of North Sea to Angola (Manning and Holthuis 1981, d'Udekem d'Acoz 1999, Muñoz et al. 2012), including the Azores (Fransen 1991), Canary (González 2016, 2018) and Cape Verde islands (Fransen 1991). Mediterranean: many records from both western and eastern basins (Pipitone and Tumbiolo 1993, d'Udekem d'Acoz 1999).

**Habitat.** On sandy shell bottoms (Fransen 1991), coralligenous and detrital substrates (Moncharmont 1979), and muddy sandy bottoms (García Raso 1984). Between 18 (García Raso 1984) and 206 m depth (present work).

**Remarks.** The holotype or specimens preserved under the name *Arctopsis lanata*, and from the topotypical locality, are no longer available, and therefore no comparison is possible. The original description by Lamarck (1801: 155) was very vague and without illustration, but in White (1857: 21, plate I,2) there is a figure that closely resembles *P. armata*. Consequently, following the opinion of Holthuis (1962) and China (1964: 208–209, Opinion 708, ICZN), as mentioned above, the generic name *Arctopsis* and the specific name *lanata* are suppressed. Thus, the valid name of the genus is *Pisa* (Lamarck 1814), and the type species is *Maja armata* (Latreille 1803).

***Pisa chiragra*** (Fabricius, 1775) n. comb.  
(Figs 5C1–3, 6F, 7A3, 8D)

*Cancer cruentatus* Linnaeus, 1758 (suppressed under ICZN Opinion 522).

*Cancer chiragra* Fabricius, 1775 (superseded combination).

*Lissa chiragra* Fabricius, 1775 (superseded combination).

**Material examined.** Spain, Balearic Islands, Maó, ovig ♀ 23.5×28.7 mm, ♀ 20×27 mm, MEDITS0522 stn 238, 57 m, 39.82°N 4.20°E, 2 Jul. 2022, IEOCD-MEDITS22/295; Balearic Islands, Sóller, ovig ♀, damaged, MEDITS0522, stn 201, 60 m, 39.86°N 2.77°E, 21 Jun. 2022, IEOCD-MEDITS22/296; Murcia, Cartagena, ovig ♀, 25.3×24.3 mm, 44 m, 37.53°N 0.80°W, 13 May 2004, ICMD001011; Murcia, Cartagena, ovig ♀, 31.9×32.4 mm, 46 m, 37.48°N 0.37°W, 2 Jun. 2000, ICMD297/2000; Balearic Islands, Santanyi, juv ♀, 10.1×13.5 mm, MEDITS0522, stn 93, 195 m, 39.31°N 3.26°E, 22 Jun. 2022, IEOCD-MEDITS22/300.

**Distribution.** Eastern Atlantic: south of Portugal (Sines, and Portimão) (Guerra and Gaudêncio 1981). Mediterranean: many records from both western and eastern basins (Pipitone and Tumbiolo 1993; d'Udekem d'Acoz 1999).

**Habitat.** On coralline bottoms (Pérès and Picard 1964); detrital substrates and mud bottoms (Števcíć 1990). Between 14 (Števcíć 1990) and 195 m depth (present work), mainly between 20 and 40 m (Zariquiey Álvarez 1968).

**Remarks.** The morphological characters used by Leach (1815) to separate *Lissa chiragra* (Fabricius, 1775) from *Pisa* species were carapace naked, rostral spines contiguous and chelipeds not denticulate on the

inside. However, after analysis, it may be concluded that these characters are no longer valid or sufficiently distinctive. The carapace is practically naked (with few hooked and mace setae) in *P. hirticornis*, *P. muscosa*, *P. tetraodon* and *P. chiragra* n. comb., while in *P. armata* and *P. nodipes* it has dense short, pile-like setae with clusters of larger hook setae on the raised areas (bumps, spines, etc.). The rostral spines meet from the base and diverge at the apex in all *Pisa* species. The same pattern is observed in *P. chiragra* n. comb., where the rostral spines remain fused but are truncated at the apex. *P. chiragra* n. comb. exhibits small lobes or teeth on the fixed and movable fingers of P1, which are not visible when the chelipeds are closed, while the other species have more pronounced teeth. Additionally, some adult males of *P. chiragra* n. comb. may display a significant hiatus (gap) in their chelipeds, similar to *P. nodipes* and *P. tetraodon*.

Within the Epiplatidae, the presence of spines and tubercles in many of the carapace regions is very common. A detailed study of the spine-tubercles distributed over the carapace of the *Pisa* species shows a similar configuration (Fig. 5). What sets *P. chiragra* n. comb. apart from all other *Pisa* species is the presence of numerous robust tubercles on its carapace. These tubercles are further covered by smaller-sized ones, giving them the appearance of calcareous algae formations. This distinctive characteristic distinguishes *P. chiragra* n. comb. from other species within the genus. The development of tubercles in *P. chiragra* n. comb. can vary, and it may be related to specimen size. Larger individuals tend to have larger and more massive tubercles (Figs 5C2–3) than smaller individuals (Fig. 5C1). Thus, the carapace of juvenile individuals of *P. chiragra* n. comb. exhibits similarities with that of *P. nodipes* (Figs 5C1 and B).

All *Pisa* species have a prominent and large mesogastric protuberance and several cardiac protuberances along the longitudinal mesial line. Additionally, *P. armata* has an intestinal acute spine (Figs 5A, 6A), *P. nodipes* has a well-developed blunt tubercle (Figs 5B, 6B), and *P. chiragra* n. comb. has a large bilobed tubercle (Figs 5C1–C3, 6F). Anteriorly to the largest gastric protuberance, a small tubercle is present in *P. muscosa*, *P. tetraodon*, *P. armata*, *P. nodipes* and *P. hirticornis*. However, in *P. chiragra* n. comb. (Figs 5A–F), this feature is not clearly distinguishable because the massive gastric tubercle is composed of smaller tubercles. Nonetheless, in some specimens of *P. chiragra* n. comb. two small tubercles may be observed (Fig. 5C2, IEOCD-MEDITS22/295).

All *Pisa* species have some well-defined small tubercles arranged transversally on the protogastric region. *Pisa muscosa* has four, *P. tetraodon*, *P. hirticornis* and *P. chiragra* n. comb. have five (two lateral ones on both sides and one in the middle, somewhat in front), while *P. nodipes* and *P. armata* show four poorly defined tubercles (with a very slightly protruding mesial area, but no tubercle) (Figs 5A–F).

The lateral margin of the branchial region in *P. nodipes* and *P. armata* is characterized by having only

one posterior spine. In *P. tetraodon*, *P. hirticornis*, and *P. muscosa*, there are three spines, with the anterior one being smaller and sometimes lobed as in *P. muscosa*. In the case of *P. chiragra* n. comb., the lateral margin of the branchial region is composed of big lobes that are compounded by smaller tubercles.

There are distinct differences among *Pisa* species in the morphology of the posterior branchial spine on the carapace and towards the inner side (on both sides of the cardiac tubercle). *P. muscosa* has a single protruding lobe or blunt spine, while *P. armata* and *P. nodipes* have a slightly protruding area in this region. *P. tetraodon* and *P. hirticornis* have two protruding areas, with *P. tetraodon* showing a more pronounced outer area and *P. hirticornis* showing a more pronounced inner area. In some cases, the outer area may be indistinguishable, particularly in small specimens, if the seta has fallen. *P. chiragra* n. comb. is characterized by having large metabranchial tubercles.

The anterior inner branchial region (epibranchial) also exhibits differences among these species: *P. nodipes* and *P. armata* both have two blunt protuberances, with the posterior-outer protuberance being larger and bilobed or trilobed, while in front of it there is another smaller protuberance. *P. tetraodon* has a single protuberance, and in front of it there is a small non-protruding defined area with hooked setae. *P. muscosa* and *P. hirticornis* have a single protuberance each, while *P. chiragra* n. comb. has a large tuberculate bulk in this region.

The male G1 of *P. chiragra* n. comb. exhibits morphological similarities to that of other species within the genus *Pisa*. It is characterized by a widened distal part, with the outer side being larger and protruding upwards compared with the inner side (Fig. 8D, Fig. 156c in Zariquiey Álvarez 1968).

Moreover, Guerao et al. (2003) described and illustrated the two zoeae, megalopa and first crab stage of *Pisa chiragra* n. comb. (as *Lissa chiragra*) and compared them with other known larval descriptions of Pisinae. They concluded that the morphology of all these larval stages is very similar to that of the other larvae of the genus *Pisa*. In fact, they mentioned that it is impossible to separate the larvae of *L. chiragra* from those of *Pisa*. This observation, along with the molecular evidence and analysis of adult morphological characters discussed above, further supports the inclusion of *Lissa chiragra* within the genus *Pisa*.

***Pisa hirticornis* (Herbst, 1804)**  
(Figs 5E, 6D)

*Cancer hirticornis* Herbst, 1804 (superseded combination).  
*Maia corallina* Risso, 1816 (junior subjective synonym).  
*Pisa corallina* (Risso, 1816) (junior subjective synonym).  
*Pisa intermedia* Nardo, 1847 (nomen nudum); Nardo, 1869 (junior subjective synonym).

*Material examined.* Spain, Girona, Cadaqués, ♀ 28.5×30.4 mm, 43.28°N 3.28°E, 22 Jul. 1953, ICMZ2040/2016; ♂ 25.2×27.3 mm,

7 Nov. 1958, ICMZ2058/2016; ♀ 24.9×27.0 mm, 15 Jan. 1958, ICMZ2070/2016; ♀ 11.5×12.8 mm, ICMZ13887/2017; ♀ 9.6×10.7 mm, ♀ 9×10.5 mm, ♀ 9.2×10.9 mm, Sep. 1952, ICMZ2244, 45, 46, 47; ♀ 14×15.7 mm, ♀ 14.2×15.8 mm, ICMZ14020-21/2017.

*Distribution.* Mediterranean: western basin (Forest 1966, Zariquiey Álvarez 1968, Grippa 1993) and many records from the eastern basin (d'Udekem d'Acoz 1999). Probably absent from Alboran Sea (García Raso et al. 1987).

*Habitat.* *Posidonia* bottoms, chiefly between 5 and 10 m depth (Zariquiey Álvarez 1968), although it can reach a depth of 37 m (Lewinsohn and Holthuis 1986).

*Remarks.* *Pisa hirticornis* and *P. tetraodon* are closely related species with many similar morphological characters (Sakai 1999). They are so similar that some authors have considered them as synonyms (Nardo 1869, Pesta 1918). Forest (1966) also questioned the validity of *P. hirticornis* and suggested that it might actually represent a variable form of *P. tetraodon*. This was in line with the earlier observations by Zariquiey Álvarez (1959), who noted the similarity between *P. hirticornis*, *P. tetraodon* and *P. muscosa*. However, Forest later accepted the species status of *P. hirticornis*.

Though *P. hirticornis* is considered a good species and is supported by strong molecular evidence in the present study, a morphological review of specimens from the Zariquiey Collection (CBMR, ICM-CSIC) collected between the 1950s and the 1960s from Cadaqués (NW Mediterranean) raises questions about the relevance of all the characters that were previously assigned to *P. hirticornis* and *P. tetraodon* by Zariquiey Álvarez (1959, 1968). After examining 54 specimens of *Pisa* species from the Zariquiey Collection (see examined material), it was observed that there were some misidentifications of *P. hirticornis*. Out of the 29 individuals initially assigned to this species in the collection, only seven were confirmed to be *P. hirticornis*, while the rest were subsequently identified as *P. muscosa*. This suggests that there may have been confusion or mislabeling of specimens in the collection, leading to incorrect identifications.

It is noted that some of the characters used by Zariquiey Álvarez in his key (Zariquiey Álvarez 1959, 1968) to distinguish *P. hirticornis* from *P. tetraodon* may not be reliable features. Specifically, the description of *P. hirticornis* in the key includes “sharp hepatic spine, pointing crosswise out” (Forest 1966) and “branchial margin spines sharp and pointing out, not curved”. However, based on the examination of specimens from the Zariquiey Collection, it has been observed that these characters may not consistently differentiate between *P. hirticornis* and *P. tetraodon*. After conducting a comprehensive review of the seven examined specimens of *P. hirticornis*, we concluded that the hepatic spine is not always straight and directed outwards but may be slightly curved, especially in large specimens; and the second and third lateral spines in branchial region can also be curved. In fact, the second lateral

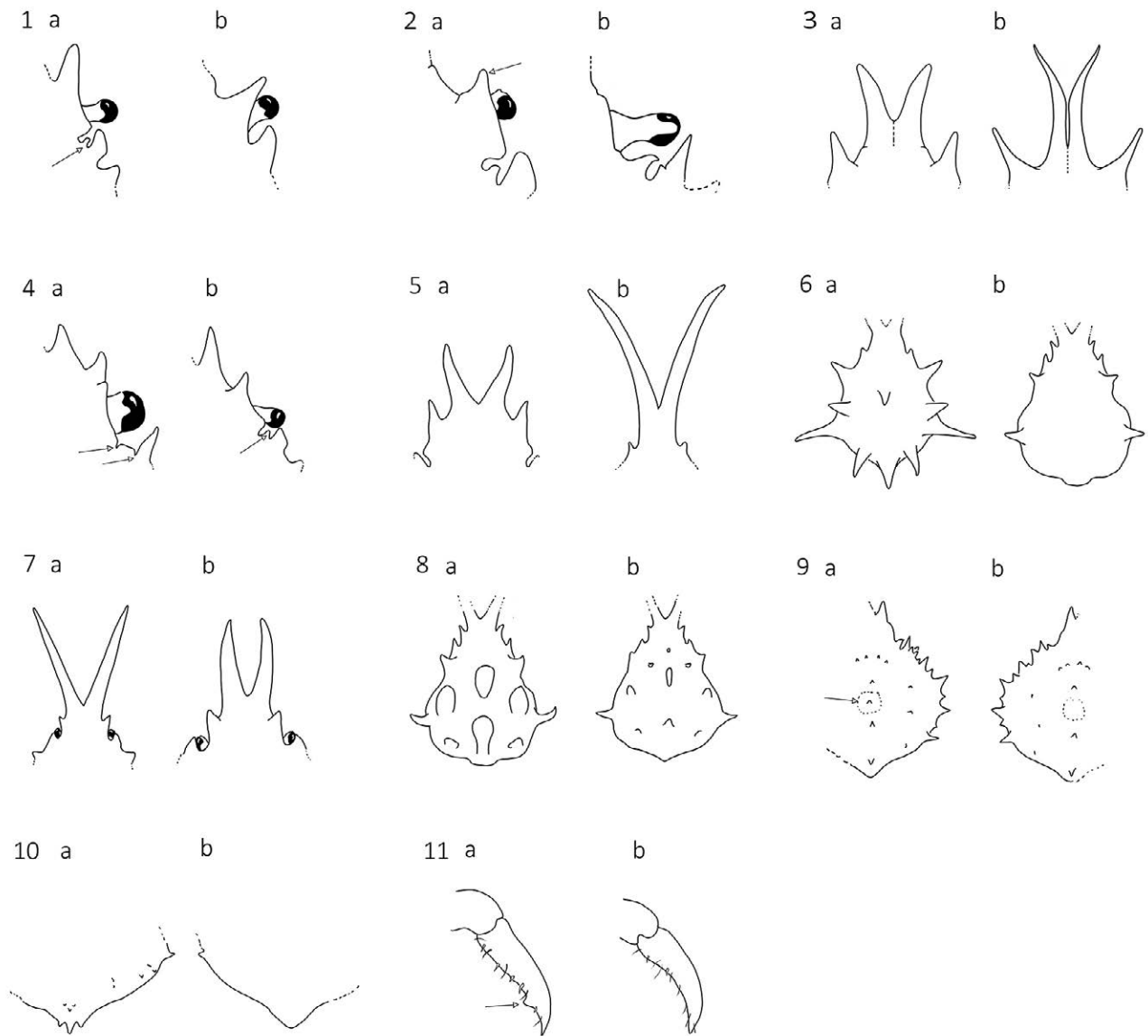


Fig. 9. – Explanatory illustrations of the key to eastern Atlantic and Mediterranean species of Pisinae (Epiplatidae).

spine is slightly curved upwards in five specimens, and in four crabs the third lateral spine is curved upwards, more markedly in large specimens. Based on our examination and analysis, we have reached the conclusion that the most reliable character for distinguishing between *P. hirticornis* and *P. tetraodon* is the morphology of the rostral spines. In *P. hirticornis*, the rostral spines are long, contiguous, and only diverge distally, while in *P. tetraodon*, the rostral spines are shorter and diverge from the middle. Additionally, we have observed that the inner setiferous tubercle of the posterior branchial region is larger in *P. hirticornis* (Forest 1966) than in *P. tetraodon*. These distinct characteristics provide a more definitive means of separating the two species.

***Pisa muscosa* (Linnaeus, 1758)**  
(Figs 5F, 6E)

*Cancer muscosa* Linnaeus, 1758 (superseded combination).  
*Maja ambigua* A. Costa, 1840 (junior subjective synonym).

*Material examined.* Spain, Girona, Cadaqués, ♂ 12×13.1 mm, 43.28°N 3.28°E, 8 May 1955, ICMZ2065/2016; ♂ 8.4×10.4 mm, 9 May 1956, ICMZ2066/2016; ♂ 13.2×14.9 mm, 16 Aug. 1948, ICMZ2251/2016; ovig ♀ 12.4×13.9 mm, ♀ 11.4×12.6 mm, 16 Aug. 1948, ICMZ2253/2016; ♀ 6.4×8.4 mm, ♂ 12.8×15.1 mm, ♂ 11.4×12.4 mm, 27 Jul. 1950, ICMZ2296/2016 and ICMZ2298/2016; ovig ♀ 11.7×13.3 mm, ♀ 13.4×14.9 mm, 3 Aug. 1954, ICMZ2234/2016 and ICMZ2235/2016; ♀ 7.2×9.8 mm, ♂ 11.7×13.1 mm, Aug. 1947, ICMZ2302/2016 and ICMZ2303/2016; ♂ 13.5×15.1 mm, Sep. 1952, ICMZ2244-47; ♀ 11.5×13.5 mm,



♀ 10.7×12 mm, ♀ 12.4×13.3 mm, ♀ 5.8×6.7 mm, ♀ 5.7×7.1 mm, Aug. 1951, ICMZ2237/2016 and ICMZ2241/2016; ♂ 12×13.2 mm, ♂ 8.6×10.1 mm, Aug. 1954, ICMZ2265/2016 and ICMZ2266/2016; ♀ 7.1×8.6 mm, ♀ 8.9×10.7 mm, 7 Sep. 1959, ICMZ1934-36/2016; Balearic Islands, Santanyi, ♂ 10×1.7 mm, MEDITS0522 stn 195, 93 m, 39.31°N 3.26°W, 22 Jun. 2022, IE-OCD-MEDTIS22/301; Balearic Islands, ♂ 14.5×15.5 mm, CANAL0209 stn 18, IEOD-PISA/3005; Menorca, Maó, ovig ♀ 14.8×17.2 mm, MAO12 stn 38, IEOD-PISA/3006; ♂ 7.1×8.2 mm, MAO12 stn 38, IEOD-PISA/3007. Mediterranean Sea, ♂ 13.4×15.6 mm, ICMZ13865/2017.

**Distribution.** Mediterranean: from Alboran Sea to Levantine Sea (d'Udekem d'Acoz 1999).

**Habitat.** Mainly among *Posidonia oceanica* rhizomes (d'Udekem d'Acoz 1999), sand and muddy sand bottoms (García Raso 1984). Mainly between 4 and 40 m depth (Zariquiey Álvarez 1968), sometimes up to 137 m (Lewinsohn and Holthuis 1986).

**Remarks.** As Zariquiey Álvarez (1959) noted, *P. muscosa* is closely related to *P. hirticornis* (referred to as *P. corallina*) and *P. tetraodon*, with a rostrum that is more similar to that of *P. hirticornis*. *P. muscosa* has a single setiferous tubercle in the posterobranchial part, not two as in *P. tetraodon* and *P. hirticornis*, although in the latter species the external one is sometimes very small. Hepatic spines are very small or even absent in *P. muscosa*; if they are present, they are always smaller than the external orbital ones, while in the other two species they are well developed and larger than the external orbital spines. Moreover, *P. hirticornis* and *P. tetraodon* have three well-differentiated laterobranchial spines, while in *P. muscosa* their development is more variable, being somewhat lobed, especially the anterior one (see Fig. 151c in Zariquiey Álvarez, 1968).

### *Pisa nodipes* Leach, 1815 (Figs 5B, 6B)

*Maia nodipes* (Leach, 1815) (superseded combination).  
*Inachus musivus* Otto, 1821 (junior subjective synonym).

**Material examined.** Spain, Cádiz, Castillo de Santa Catalina, ♂ 20×23.5 mm, 36.53°N 6.31°W, 1 Aug. 2015, IEOD-PISA/3009; ♂ 16.8×18.4 mm, IEOD-PISA/3033; Cádiz, Castillo de San Sebastián, indet, 36.52°N 6.31°W, IEOD-PISA/3032; ♀ 14.9×17.5 mm, IEOD-PISA/3034; Málaga, Cabopino, ♂ 13.8×15.7 mm, 36.50°N 4.63°W, 18 May 2005, IEOD-PISA/3008; Menorca, Maó, ♂ 9.7×10.1 mm, 72 m, 39.82°N 4.37°E, 29 Jan. 2014, ICMD000865. Portugal, Madeira, Funchal Bay, ♀ 17.7×21.9 mm, 1 May 1959, MMF 15797; Funchal fish market, ♂ 21.3×22.6 mm, 27 Jul. 1956, MMF 8838.

**Distribution.** Eastern Atlantic: from the English Channel and France to Mauritania (d'Udekem d'Acoz 1999), including Madeira (Fransen 1991) and the Canary (González 2016) and Cape Verde islands (González et al. 2017, González 2018). Mediterranean: many records from both western and eastern basins (d'Udekem d'Acoz 1999).

**Habitat.** On rocky bottoms, often with significant animal concretion; rhizomes of *Posidonia* (d'Udekem d'Acoz 1999); coralligenous bottoms; coarse sand bottoms under the influence of the current (Ledoyer 1968), detrital bottoms (Števcíć 1990). From the intertidal zone (Livory 1997) up to 100 m depth (Števcíć 1990).

**Remarks.** *P. nodipes* is morphologically and molecularly closely related to *P. armata*, but both species can be easily differentiated by the shape of the intestinal tubercle-spine, which is a blunt spine in *P. nodipes* but an acute spine in *P. armata*. However, in order to see it, one must "remove" the dense, short, pile-like setae that exist in this carapace area. *P. nodipes* also has a more developed hepatic spine and two deep sulcs in the third thoracic sternite (absent in *P. armata*).

### *Pisa tetraodon* (Pennant, 1777) (Figs 5D, 6C)

*Cancer tetraodon* Pennant, 1777 (superseded combination).  
*Arctopsis tetraodon* Pennant, 1777 (generic name suppressed).  
*Cancer hircus* Fabricius, 1781 (junior subjective synonym).  
*Cancer praedo* Herbst, 1796 (junior subjective synonym).  
*Inachus tomentosus* Rafinesque, 1814 (junior subjective synonym).  
*Pisa convexa* Brandt, 1880 (junior subjective synonym).  
*Pisa quadricornis* Brandt, 1880 (junior subjective synonym).

**Material examined.** Spain, Cádiz, Rota, ♂ 21.3×21.5 mm, 36.61°N 6.36°W, 20 Apr. 2012, IEOD-PISA/3016; Cádiz, El Chato, ♂ 22.5×23.1 mm, 36.47°N 6.26°W, 1 Sep. 2009, IEOD-PISA/3010; Cádiz, Sancti Petri, ♂ 6.6×6.8 mm, 15 Jan. 1996, ICM; Cádiz, Castillo de San Sebastián, ♂ 25.1×28 mm, 36.52°N 6.31°W, IEOD-PISA/3012; Cádiz, Castillo de Santa Catalina, ♀ 21.1×22 mm, 36.53°N 6.31°W, 15 Jun. 2015, IEOD-PISA/3011; LOCALIDAD ovig ♀ 25.8×25.2 mm, ovig ♀ 26.6×28.8 mm, ovig ♀ 26.7×27.6 mm, ovig ♀ 22.3×22.9 mm, ♂ 19.8×20.1 mm, ♂ 17.7×18.7 mm, 20 Feb. 2015, IEOD-PISA/3013; Cantabria, Playa de Oyambre, ♂ 13.2×14.1 mm, 43.39°N 4.33°W, IEOD-PISA/3014; Canary Islands, Santa Cruz de Tenerife, juv ♂ 6.3×6.7 mm, 28.46°N 16.24°W, Sep. 1986, IEOD-PISA/3035; 2 indet, 6.4×6.2 mm, 1 Sep. 1986, IEOD-PISA/3036; ♂ 13.9×15.9 mm, 1 Sep. 1986, IEOD-PISA/3037; Alicante, Calpe, indet, 18 Sep. 2015; Granada, La Heradura, ♂ 20.8×20.1 mm, 3–4 m, 36.75°N 3.77°W, 28 Oct. 2006, IEOD-PISA/3038. Portugal, Madeira, Funchal Bay, ♀ 19×19.9 mm, 18 Nov. 1964, MMF 23458; Madeira, Caniçal, Baía d'Abra, ♂ 32.6×32.2 mm, 22 Jul. 1979, MMF 23312.

**Distribution.** Eastern Atlantic: from the Isle of Man, west of Ireland and English Channel to Mauritania (d'Udekem d'Acoz 1999), including the Canary Islands (González 2016, 2018). Mediterranean: many records from both western and eastern basins (d'Udekem d'Acoz 1999).

**Habitat.** On *Posidonia oceanica* bottoms (Zariquiey Álvarez 1968), rocky bottoms, rocky bottoms with algae, sand bottoms with rocks (García Raso 1984), sometimes associated with *Cystoseira* spp. or intertidal (Livory 1997, d'Udekem d'Acoz 1999). From 3 to 100 m depth (Zariquiey Álvarez 1968, Noël 2016, this work).

*Remarks.* *Pisa tetraodon* is the most common species within the genus *Pisa* and is found on shallow bottoms of rocks, algae and seagrasses. For comparative morphological comments, see the above observations on *P. hirticornis* and *P. muscosa*.

#### IDENTIFICATION KEY TO EASTERN ATLANTIC AND MEDITERRANEAN SPECIES OF PISINAE (EPIALTIIDAE)

- 1 Presence of intercalated spine or lobe (sometimes reduced to a broad rim, or intercalary area, delimited by two fissures), between posterior margin of supraorbital margin and postorbital spine or lobe (Fig. 9.1a) 2
  - Absence of intercalated spine, lobe, or intercalary area (Fig. 9.1b) 6
- 2 Supraorbital margin prolonged anteriorly by an apophysis or lobe (rounded or spiniform) (Fig. 9.2a) 3
  - Supraorbital margin not prolonged anteriorly by a spine. Reduced intercalary lobe (Fig. 9.2b) 10 (*Apiomithrax* Rathbun, 1897)
- 3 Rostral spines relatively short, divergent from the base or close to it (Fig. 9.3a) 4
  - Rostral spines contiguous, or fused, at the base and divergent next to the tip (Fig. 9.3b) 11 (*Pisa* Leach, 1814)
- 4 With a broad intercalary lobe “rim” (not spine or lobe proper) delimited by two fissures (Fig. 9.4a) 16 (*Herbstia* H. Milne Edwards, 1834)
  - With a small, intercalated spine (Fig. 9.4b) 5 (*Afropisa* n. gen.)
- 5 Only one lateral spine on branchial region of carapace (Fig. 5G) *Afropisa carinimana* (Miers, 1879) n. comb.
  - Four lateral spines (first two close together) on lateral region of carapace (Fig. 5H) *Afropisa sanctaehelenae* (Chace, 1966) n. comb.
  - Two spines on lateral region of carapace. Short and slightly divergent rostral spines, separated from the base with a central U-shaped area (Fig. 5I) *Afropisa calva* (Forest and Guinot, 1966) n. comb.
- 6 Rostral spines short, with acute sinus (Fig. 9.5a) *Micropisa ovata* Stimpson, 1857
  - Rostral spines very long and divergent (Fig. 9.5b) 7
- 7 Carapace rather swollen, strongly spinose; rostrum and carapace spines very long and acute. Rostral spines, divergent, only fused at their base (Fig. 9.6a) *Anamathia rissoana* (Roux, 1828 [in P. Roux, 1828-1830])
  - Carapace distinctly pyriform, with shorter spines (compared with those of *Anamathia*) and strong, raised plate-like structures in large adult specimens (instead of some spines) (Fig. 9.8a). Rostral spines slender and long, divergent from its base (Fig. 9.6b) 8
- 8 Rostral spines long, slightly longer than or equal to half carapace length (Fig. 9.7a); basal antennal segment with straight to gently convex outer margin 9
  - Rostral spines shorter than half carapace length (Fig. 9.7b); basal antennal segment with convex outer margin *Scyramathia hertwigi* Doflein, in Chun 1900
- 9 With weak or relatively distinct plates on carapace (Fig. 9.8a); lateral branchial spine sharp, pointing laterally, slightly upwards; pterygostomial region with plate-like granules on outer margins; P2 merus length 11.8–14.0 times in width; P5 merus length 5.5–7.3 times in width *Scyramathia carpenteri* (Norman, in Thomson 1873)
  - With weak plates on carapace; lateral branchial spines sharp, pointing outwards (Fig. 9.8b); pterygostomial region with distinct granules on outer margins; P2 merus length 19.5–20.5 times width; P5 merus length 8.0–9.6 times width *Scyramathia tenuipes* Lee, Richer de Forges and Ng, 2020
- 10 Presence of one spiniform urogastric tubercle and four prominent tubercles arranged in a transverse row across the level of the gastric region (Fig. 9.9a) *Apiomithrax bocagei* (Ozorio, 1887)
  - Absence of urogastric tubercle and three prominent tubercles arranged in a transverse row across the level of the gastric region (Fig. 9.9b) *Apiomithrax violaceus* (A. Milne-Edwards, 1867)
- 11 Rostral spines apex extremity truncated, the outer ends forming a small lateral lobe or tooth. Carapace with large, bulky, tubercles, separated by deep depressions (Figs 5C, 6F) *Pisa chiragra* (Leach, 1815) n. comb.
  - Rostral spines apex acute. Without large, bulky, tubercles on the carapace 12
- 12 Lateral branchial margin with only one strong mesobranchial spine (sharp or blunt) (Figs 5A, B, 6A, B) 13
  - Lateral branchial margin with more spines or lobes (well-defined) 14
- 13 Presence of hepatic spines. Intestinal spine with sharp, pointed apex (Figs 5A, 6A) *Pisa armata* (Latreille, 1803)
  - Absence of hepatic spines. Intestinal spine with blunt and rounded apex (Figs 5B, 6B) *Pisa nodipes* (Leach, 1815)

- 14 Hepatic spines long, beyond the external orbital spine. Posterior branchial region with two setiferous tubercles 15  
 – Hepatic spines small or absent, always smaller than the external orbital spine. Posterior branchial region with only one setiferous tubercle (Figs 5F, 6E)  
*Pisa muscosa* (Linnaeus, 1758)
- 15 Rostral spines relatively short, contiguous at their base, but strongly divergent in their distal half or in the distal 2/5. Both setiferous tubercles of equal size or the outside one larger (Figs 4D, 5C)  
*Pisa tetraodon* (Pennant, 1777)  
 – Rostral spines very long and contiguous, only divergent distally. Hepatic spines usually straight and outward direct, or slightly curved. Inner setiferous tubercle larger (Figs 5E, 6D)  
*Pisa hirticornis* (Herbst, 1804)
- 16 Posterior median margin of carapace with trilobed projection in adult (or large) specimens (Fig. 9.10a). (Opposable margins of dactyli of walking legs similar to *H. nitida*)  
*Herbstia condyliata* (Fabricius, 1787)  
 – Posterior median margin of carapace with single projection (Fig. 9.10b) 17
- 17 Carapace smooth, with regions poorly defined. Upper surface of palm in males smooth. Opposable margins of dactyli of walking legs with fixed triangular teeth (Fig. 9.11a)  
*Herbstia nitida* Manning and Holthuis, 1981  
 – Carapace rugose, with regions well defined. Upper surface of palm in males with row of tubercles. Opposable margins of dactyli of walking legs lacking fixed triangular teeth (Fig. 9.11b)  
*Herbstia rubra* A. Milne-Edwards, 1869

## DISCUSSION AND CONCLUSIONS

Three of the species described as belonging to the genus *Pisa*, *P. calva*, *P. carinimana* and *P. sanctaehelenae*, share several morphological characteristics, which differentiate them from the other *Pisa* species and allow us to separate them into a new genus, *Afropisa*. The molecular analysis conducted on *A. carinimana* n. comb. confirms its distinctiveness from the genus *Pisa*. The genetic distance observed in the mitochondrial sequences, as shown in Figs 2–4, further supports its separation from *Pisa* and suggests a closer relationship with *Micropisa*.

Additionally, Stimpson (1857, in Monod 1956) pointed out that there was a generic difference in the third maxilliped, whose merus would be without a notch for the reception of the carpus in *Micropisa* but with a notch in *Pisa*, and he also mentioned that *Pisa carinimana*, which cannot be separated from *Pisa*, does not have the notch. *Afropisa carinimana* n. comb. does not have a well-differentiated lobe on the merus of the third maxilliped at the level of the carpal insertion

(Fig. 7A1, Monod 1956: Figs 658–661), as may be observed in *Pisa* (Figs 7A2, 7A3). This lobe is also absent in *A. sanctaehelenae* n. comb. (Chace 1966: Fig. 14c), *A. calva* n. comb. (Forest and Guinot 1966: Fig. 11c) and *Micropisa ovata* Stimpson, 1857 (Monod 1956: Fig. 674).

The rostral spines remain close together until near the tip in *Pisa*, while they are totally joined at the base and diverge very basally in *Afropisa* n. gen. The basal antennal segment has a single tubercle-shape tooth on the lower-outer margin (somewhat more developed and prominent in *P. muscosa*), whereas the *Afropisa* n. gen. has a vertically elongated tooth. On this same segment, *Pisa* species possess a small antero-outer tooth that is not visible from a dorsal view of the specimen while, for *Afropisa*, this tooth is elongated and visible from a dorsal view. For *P. muscosa* this tooth is like that of *A. carinimana* n. comb. but is not visible because of its position behind the rostral spines.

All species in the genus *Pisa* sensu stricto share the presence of a pair of tubercles in the pterygostomial region. In contrast, *Afropisa* n. gen. typically has three tubercles in this region. The new genus also lacks well-defined tubercles on the protogastric area (except in *A. calva* n. comb.) in contrast to *Pisa*.

The morphology of the first gonopod is also a distinguishing feature between these two genera. In addition, it is worth noting that the adults of the three species included in the new genus are relatively small.

However, further molecular analyses of *A. calva* n. comb. and *A. sanctaehelenae* n. comb. should be conducted in the near future to confirm their new taxonomic status through integrative taxonomy.

After conducting a comprehensive morphological study of *Lissa chiragra* specimens, reviewing relevant literature on this species, performing genetic analyses and considering the conclusions from a morphological description of its larvae by Guerao et al. (2003), it is concluded that *L. chiragra* should be reclassified under the genus *Pisa*. As *Lissa* is a monotypic genus, it is appropriate to synonymize it under the genus *Pisa*. Both morphological and molecular evidence suggest that *P. chiragra* is more closely related to *P. armata* and *P. nodipes* than to other species within the genus *Pisa*. Therefore, incorporating *P. chiragra* into the genus *Pisa* is supported by both morphological and molecular similarities.

Also based on morphological and molecular analyses, *P. hirticornis* is considered a good species that is closely related to *P. tetraodon*. While these species share many morphological characteristics, the length and point of divergence of the rostral spines serve as a stable morphological character to differentiate them. Other morphological and molecular evidence supports the distinction between *P. hirticornis* and *P. tetraodon*, further confirming their separate species status.

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