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Morphological distinction of the *Ophioderma* Müller & Troschel, 1840 species (Echinodermata: Ophiuroidea: Ophiacanthida: Ophiodermatidae) from the Algerian west coast

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Abstract

Ophioderma longicaudum (Bruzelius, 1805) is a very common brittlestar in the Mediterranean Sea that had been considered as a complex of cryptic species since 2009. Recently, five species were separated from this complex, but they remain morphologically very close. The aim of this study is to attempt for the first time to identify the species of *Ophioderma* found at the Algerian west coast, using morphological and morphometric analysis. A total of 67 individuals of *Ophioderma* species were collected from three stations at the Mostaganem coast (Salamandre, Stidia-East and Stidia-West) during 2020 and 2021 and between 1.5 and 8 m depth. The morphological features showed a strong variability between the analysed individuals. Some resembled *O. hybridum* Stöhr, Weber, Boissin & Chenuil, 2020, others *O. zibrowii* Stöhr, Weber, Boissin & Chenuil, 2020 and some *O. longicaudum* (Bruzelius, 1805). Few resembled *O. africanum* Stöhr, Weber, Boissin & Chenuil, 2020 or *O. guineense* Greeff, 1882. The morphometric study displayed a significant discrimination between individuals and confirmed the morphological results suggesting that.

Key words: Brittlestars, Cryptic species, Biodiversity, Mediterranean Sea, Algerian basin

Introduction

Brittlestars, snakestars and basketstars are very common groups of echinoderms, they inhabit all marine habitats from intertidal reefs to 6500 m depth (Smith *et al.* 1995; O'Hara *et al.* 2017). They represent a major component of the benthic fauna, adopting different dispersal strategies. Moreover, they are involved in different trophic levels (Thuy & Stöhr 2016; Alitto *et al.* 2018). Ophiuroidea is the most diverse and largest class of echinoderms, comprising about 2126 species (Stöhr *et al.* 2022) and it is considered as a model taxon to analyse global patterns of marine species diversity (Stöhr *et al.* 2012; Woolley *et al.* 2016; Boissin *et al.* 2017).

Ophioderma longicaudum (Bruzelius, 1805) was described more than two centuries ago. It was known for its high variable morphology and as spawner species. In addition to spawning (eggs and sperm are shed into the water column where fertilization and development occurs), another mode of reproduction was discovered in 2009 which is the brooding where eggs develop in gastrovascular cavity of parent. It was suspected to be a complex of cryptic species, under the name of *O. longicauda* and their morphological differences were interpreted as intraspecific variability (Fenaux 1972; Stöhr *et al.* 2009; Boissin *et al.* 2011; Stöhr *et al.* 2020). Then, six mitochondrial genes (COI) were differentiated from this species complex revealing three highly distinct lineages (Weber et al. 2014, 2015, 2017, 2019). Recently, five species were formally described, of which, two are brooders (*Ophioderma hybridum* Stöhr, Weber, Boissin & Chenuil, 2020 and *Ophioderma zibrowii* Stöhr, Weber, Boissin & Chenuil, 2020) and three are broadcast spawners (*Ophioderma longicaudum*, *Ophioderma guineense* Greeff, 1882 and *Ophioderma africanum* Stöhr, Weber, Boissin & Chenuil, 2020).

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According to Stöhr *et al.* (2020), the name of *O. longicauda* was accepted as *O. longicaudum*. The other four species show some morphological differences from the latter: 1. *O. guineense* has a single, flat dorsal arm plates, a higher number of arm spines and a light coloration of the ventral side, 2. *O. africanum* has a small number of oral papillae, 3. *O. zibrowii* can be recognized mostly by a naked radial shield, a single and flat dorsal arm plates, and usually by a green pigmentation and 4. *O. hybridum* is morphologically the most variable, sharing characteristics with *O. longicaudum* and *O. zibrowii* and differs mainly from the former by its small disc (Stöhr *et al.* 2020). These four species have in common dark and/or white spots on the distal edge of their dorsal arm plates.

Ophioderma longicaudum was studied in other fields such as physiology (Weber *et al.* 2013), morphology (Thuy & Stöhr 2016) and ecology (Mulyaningsih *et al.* 2020). In Algeria, studies on *O. longicaudum* are almost non-existent.

The main goal of this study is to identify the species of *Ophioderma* collected at three stations off the coast of Algeria. This work is a first contribution to the systematic study of the *Ophioderma* species in the west Algerian coast (Alboran Sea), where data were lacking, using the morphological criteria already established by Stöhr *et al.* (2020). We attempt to explain the morphological variability, to test and to improve the morphological identification by the morphometric analysis.

Material and methods

A sample of 67 individuals of *Ophioderma* species were collected from three stations in the Mostaganem area, Algeria (Table 1; Figure 1). Sampling was carried out between 2020 and 2021 during the following months: November, March, May, June, August and September between 1.5 and 8 m depth, by night free diving, because of the shade-seeking behaviour of these species (Hendler *et al.* 1995; Sönke & Kier 1999). After collection, the individuals were transported immediately to the Laboratory of Protection and Valorisation of Coastal Marine Resources and Molecular Systematics (LPVCMRMS, University of Mostaganem) in plastic containers filled with seawater and small rocks taken from the biotope of each station. In the laboratory, individuals were kept alive until treatment. The dorsal and ventral sides of each individual were photographed alive using a Canon EOS 1200D camera. The disc diameter was measured from the dorsal side, represented by the average of the distances between the radial shields and the interradius [$dd = (d_1+d_2)/2$] (Figure 2A). The length of the intact and unregenerated arms, the proximal arm width and the interradius width (Figure 2A) were measured using a calliper (± 0.01 mm). They represented the average of the five measurements taken clockwise from the madreporite. The individuals were anaesthetized with Magnesium Chloride ($MgCl_2$ 1% in sea water) then air-dried to be identified morphologically.

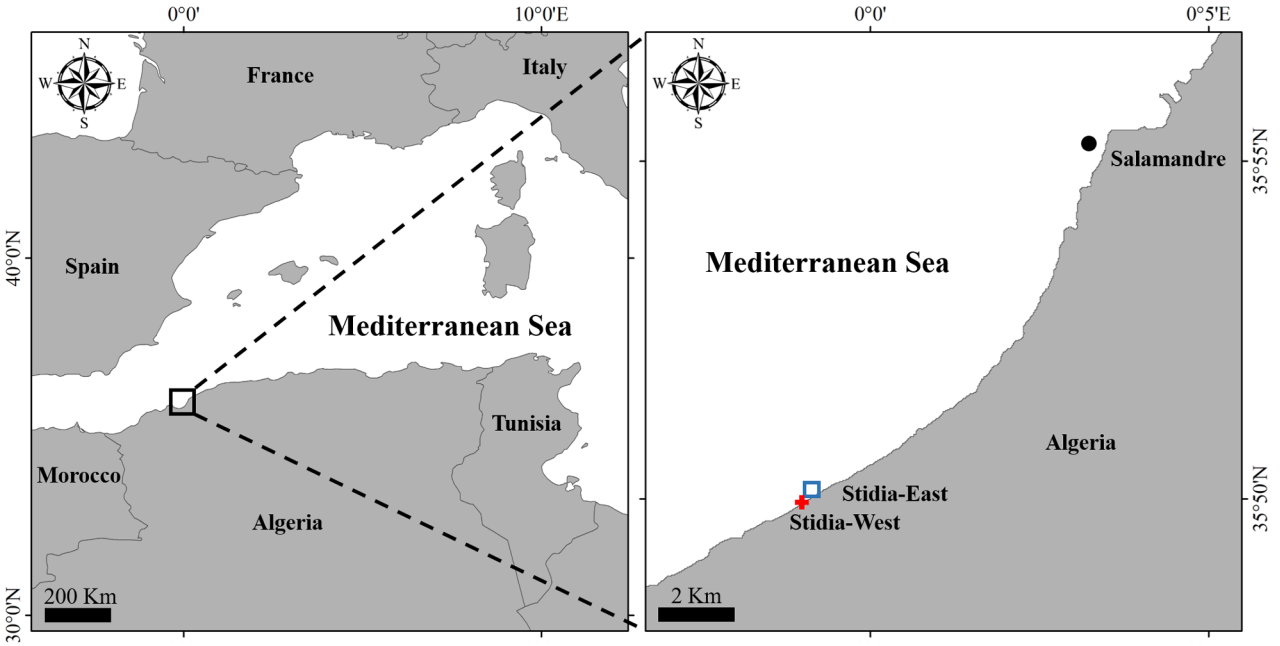

FIGURE 1. Geographical location of the sampling stations of the *Ophioderma* species. (Salamndre ●, Stidia-East □ and Stidia-West +).

TABLE 1. Locations and biotope characteristics of *Ophioderma* individuals collected at the Algerian west coast

Station	N	Catalogue number	D (m)	Geographical coordinates	Biotope
Salamandre	13	LPVCMRMS2020.601–LPVCMRMS2020.616	7	0°3.248′ E; 35°55.283′ N	Artificial rocks or rip rap seawalls
Stidia-East	48	LPVCMRMS2021.623–LPVCMRMS2021.667	3–8	0°0.830′ O; 35°50.061′ N	Calcareous beachrock/ platforms
Stidia-West	6	LPVCMRMS2020.617–LPVCMRMS2020.622	1.5	0°0.940′ O; 35°48.968′ N	Calcareous stones

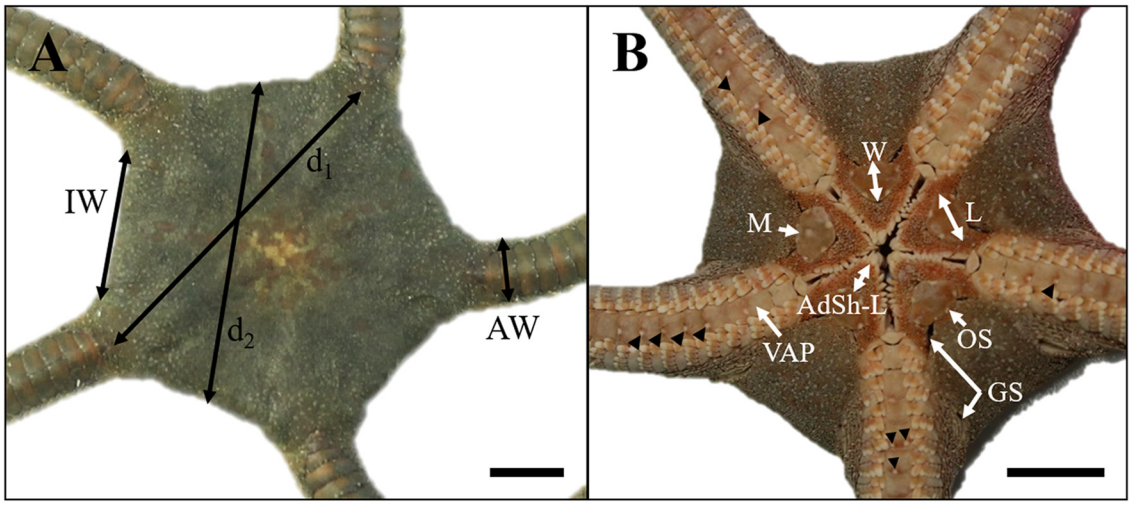

FIGURE 2. Measurements taken from dorsal (A) and ventral (B) side of *Ophioderma* species. IW: Interraduis Width. AW: Arm Width. d1 and d2: large and small disc diameters. M: Madreporite. W: Width and L: Length of oral shield and madreporite. OS: Oral Shied. AdSh-L: Adoral Shield Length. GS: Genital Slit. VAP: Ventral Arm Plates. Small black narrow: white spots on VAP. Scale bare = 5 mm

In order to identify the species composition of *Ophioderma* species in the Algerian west coast, nine identification keys described by Stöhr *et al.* (2020) were used: 1. multiplication and 2. thickness of dorsal arm plates, 3. number of arm spines, 4. radial shield, 5. colour of dorsal disc and distal edge of dorsal arm plates, 6. colour of ventral disc, 7. number of oral papillae, 8. period and 9. mode of reproduction. Nevertheless, for the last two characters only females collected during the reproduction period [late spring and summer (Stöhr *et al.* 2009; Weber *et al.* 2014; Stöhr *et al.* 2020)] were applicable.

Determination of the mode of reproduction was based on the histological analysis of the gonads and the period of reproduction. Gonads removed were fixed in 10% formalin, dehydrated in a descending series of alcohol baths, clarified with xylene, impregnated and embedded in paraffin, sectioned at 5 µm, stained with haematoxylin-eosin. The observations were carried out using a microscope (Leica DMLP type) with an attached camera.

As the occurrence of brooding is limited to the reproduction period (Stöhr *et al.* 2020) only females collected in March, May, June, August and September were considered. The presence of larvae in genital bursae of each individual was checked. Partially spawned and post-spawned females were considered as spawners. In the case of mature gonads if maturity was reached during the brooding period, they were considered brooders if it was reached during the spawning period, they were therefore considered spawners.

Additionally, a morphometric analysis was carried out on adult individual originating from the three localities (Salamandre, Stidia-East and Stidia-West) considering 10 variables (measurements). Nine variables were quantitative, of which three were performed on the living individuals (mentioned above) and six were measured on the photos taken previously using ImageJ software (± 0.001 mm). The following variables represent the average of measurements taken clockwise from the madreporite. These variables were: madreporite length, madreporite width, ratio of madreporite width to length, oral shield length, oral shield width, adoral shield length (Figure 2B). To eliminate the size effect all measurements were controlled for disc diameter. Only one qualitative variable was considered which is the presence or absence of white spots on the ventral arm plates (Figure 2B). A Canonical Variates Analysis (CVA) was performed on these data in order to check the geographical effect on the individuals of *Ophioderma* species. The scatter plot was graphed using Past v 1.93 software. A test of λ-Wilk by an approximation of the χ^2 was carried out with the same software.

Results

Morphological analysis

The analysed individuals showed great morphological variability. Dorsal arm plates of three types: single, multiple or two pieces per joint, sometimes tumid, weakly tumid or flat. Distal edges of dorsal arm plates mainly spotted with white and dark (Table 2; Figure 3). Most individuals were olive and brown on both dorsal and ventral discs but many variations were observed, such as darkish and reddish disc on the dorsal side and cream to orange on ventral one (Table 3; Figure 4–5). Radial shield of three types: covered with granules (Figure 6A), naked (Figure 6B) and mixed, the latter means that individuals had naked and covered radial shield (Figure 6C). Oral papillae between 6 and 13. Arm spines from 7 to 13. Individuals with disc diameter less than 16 mm had between 7 and 10 spines, for those with disc diameter between 16 and 27 the spines were between 7 and 13. Some individuals had 12 or 13 spines, the disc diameter was over 22 mm.

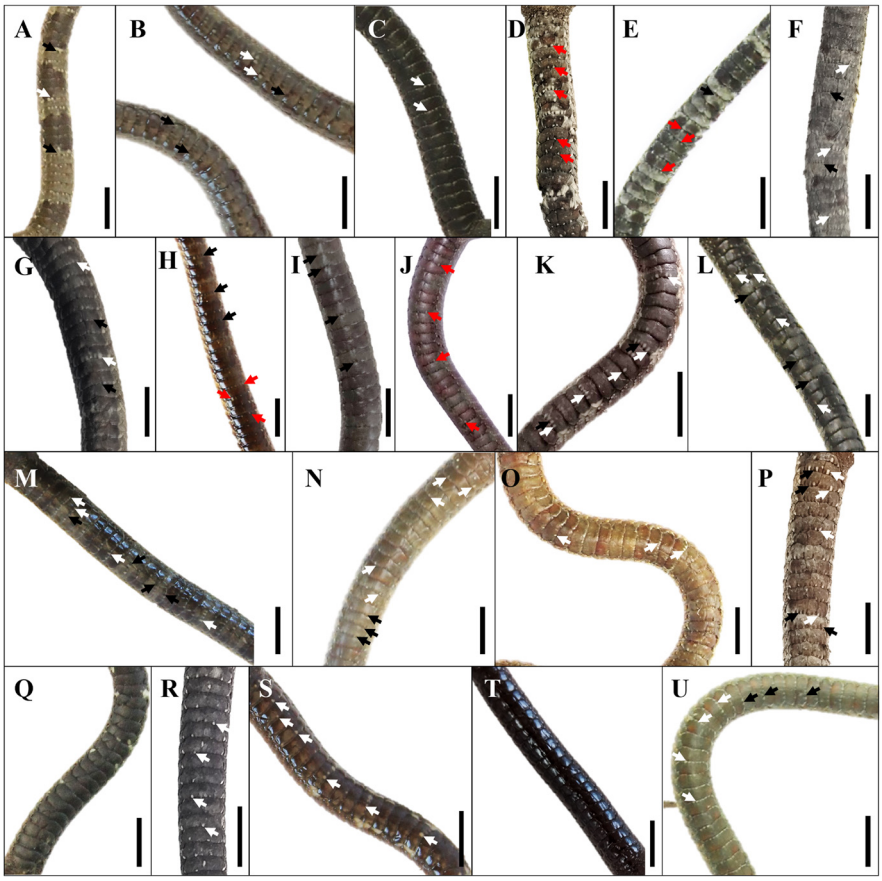

FIGURE 3. Morphological variation of the dorsal arm plates distal edge of *Ophioderma* species. Letters refer to the description in Table 2. The black arrows show dark spots. The white arrows show white spots. The red arrows show the white spots surrounded by dark. Scale bare = 0.5 mm.

TABLE 2. Dorsal arm plates distal edge description of the *Ophioderma* species from the Algeria wesat coast. The letters of the code column refer to those in Figure 3.

DAP : Dorsal Arm Plates distal edge	Code
Straight, irregular, distally concave, sharp, large white spots or small dark spots on the DAP gray bands, on some DAP alternating dark and white spots	A
Straight, blunt, dark spots, few white spots on the proximal DAP	B
Straight, concave, blunt, small white spots	C
Concave, straight, sharp, large white spots surrounded by dark or dark spots	D
Straight, concave, somewhat blunt, very small white spots surrounded by dark	E

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TABLE 2.(Continued)

DAP : Dorsal Arm Plates distal edge	Code
Straight, irregular, sharp, large white spots interspersed with dark, sometimes alternating dark and white spots	F
Concave, straight, somewhat blunt, small dark spots or large white spots on some DAP	G
Straight, blunt, small dark spots and few white spots surrounded by dark	H
Concave, irregular, somewhat blunt, shade of small dark spots on some DAP	I
Concave, straight, blunt, white spots surrounded by dark on some DAP	J
Straight, concave, blunt, large white spots or small dark spots sometimes alternating of both	K
Straight, concave, blunt, some white or dark spots on some distal DAP	L
Straight, irregular, distally concave, sharp, large white spots or small dark spots, on some DAP alternating dark and white spots	M
Straight, irregular, blunt, few white spots and shade of dark ones on some DAP	N
Concave, straight, irregular, blunt, rare white spots on some distal DAP	O
Straight, irregular, distally concave, blunt, large white or small dark spots on some DAP alternating dark and white spots	P
Concave, irregular, sharp, unspotted	Q
Straight, concave, blunt, few white spots	R
Straight, concave, irregular, sharp, large white spots on some DAP	S
Straight, irregular, blunt, unspotted	T
Straight, concave, sharp, alternating of very small white and dark spots	U

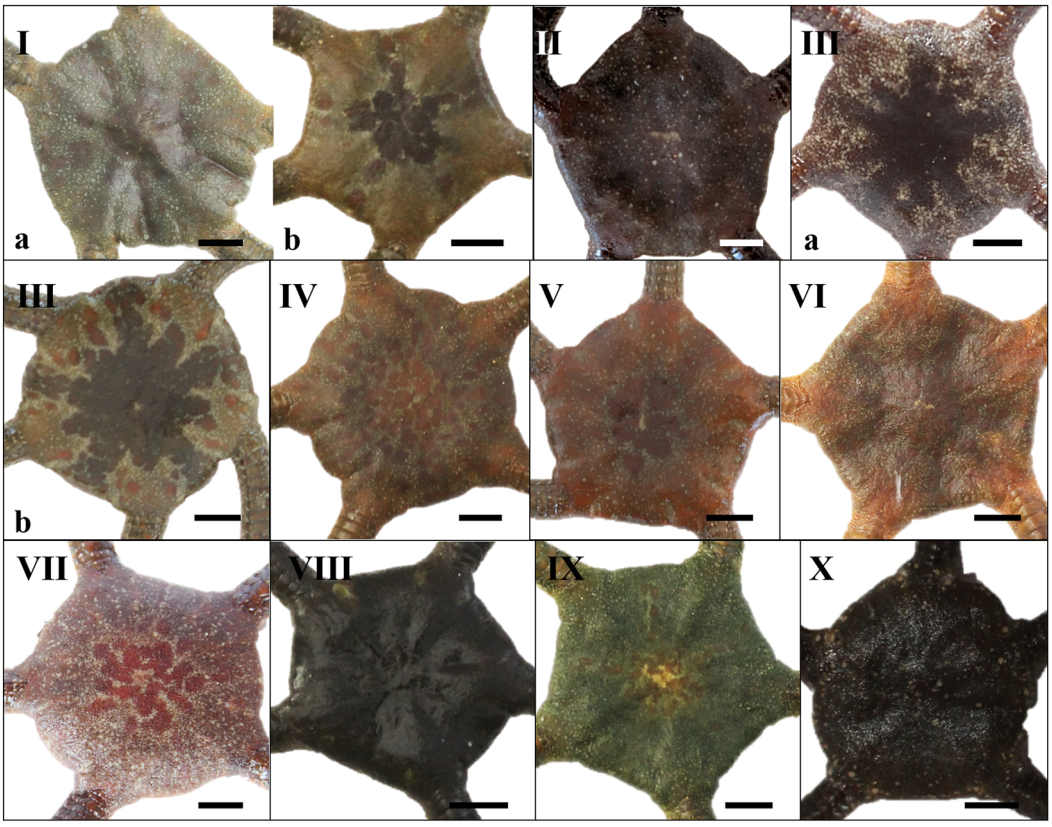

FIGURE 4. Dorsal disc colour of the Ophioderma species. Roman numerals refer to the description in Table 3. I: The general description olive (a) and brown (b) discs of type I. (c) olive disc with white spots, (d) degradation of dark brown to cream. III: (a) The general description of type III, (b) As dorsal disc but turns to creamy. IV: (a) The general description of type IV, (b) Cream yellow to orange disc. VIII: (a) The general description of type VIII, (b) disc with an orange pattern. CRS: Covered Radial Shield. NRS: Naked Radial Shield. Scale bare = 0.5 mm.

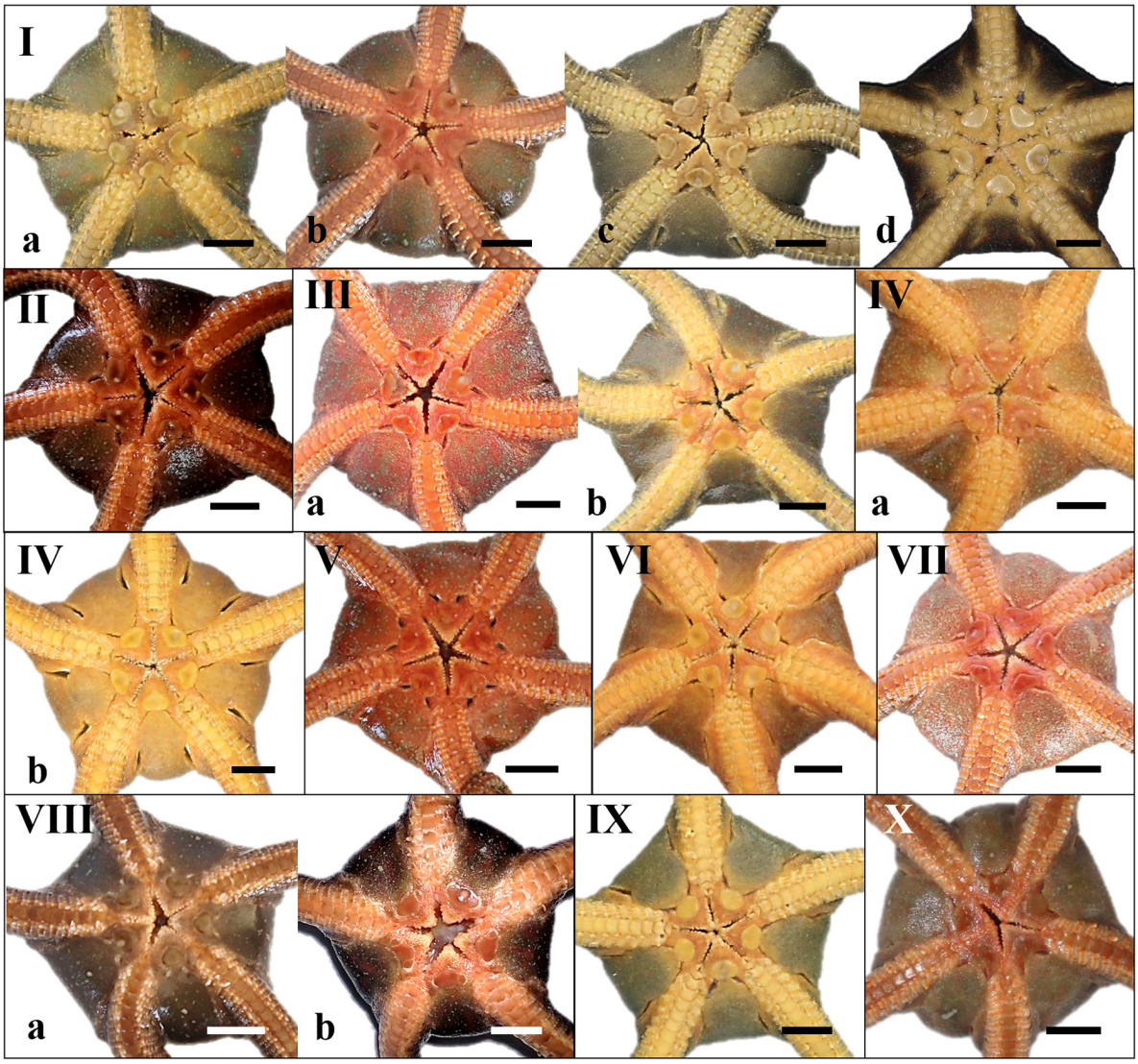

FIGURE 5. Ventral disc colour of the Ophioderma species. Roman numerals refer to the description of dorsal colour in Table 3. Scale bare = 0.5 mm.

The detailed morphological descriptions of the 67 individuals collected from the three stations are grouped in Tables 2–4 and Figure 3–6. The number of oral papillae is given as an interval, the most frequent number is indicated just after the interval followed by its frequency of appearance between brackets (e.g. individual LPVCMRMS2021.652 had between 7 and 11 papillae and the number 8 occurred five times Table 4).

Based only on morphological criteria (sensu Stöhr *et al.* 2020), it was difficult to identify our individuals because each one showed an overlapping and interfering character states with those characterising several species of *Ophioderma*. For this reason, in the last column of Table 4, we noted the criteria in common with each species as described by Stöhr *et al.* (2020) (e.g. the first individual shares five criteria with *O. hybridum* and four with *O. longicaudum*). Because of the large morphological variability of our sample, we separated in two columns the colour of the dorsal side of the disc from that of the arm plates distal edge.

TABLE 3. Dorsal disc colour description of the Algerian west coast species of *Ophioderma*. Roman numerals and legend refer to those in Figure 4.

Dorsal colour	Code
Olive green (a) or brown (b), dark pattern in the middle of the disc, sometimes stuck together and scattered, in the inter-radial zone sometimes in 2 rows, white spots dispersed on disc, some had large white patches on disc centre	I
Shade of brown, large white patches on the disc	II
Shade of brown (a) and olive green (b), vivid colour, variegated white, dark and reddish orange patches	III
Variegated green, brown and white, brown and orange spots surrounded by dark or white	IV
Reddish green, brown and orange patches, white spots, some granules are rubbed off the discs	V
Reddish brown, white spots	VI
Green to light brown, reddish brown patches, white spots	VII
Blackish brown, some (not showed in the Figure 4) had white spots and brown patches in the middle of the disc	VIII
Green, small dark and white spots	IX
Shade of brown, white spots surrounded by dark, a series of white spots on the edge of the disc forming a ribbon	X

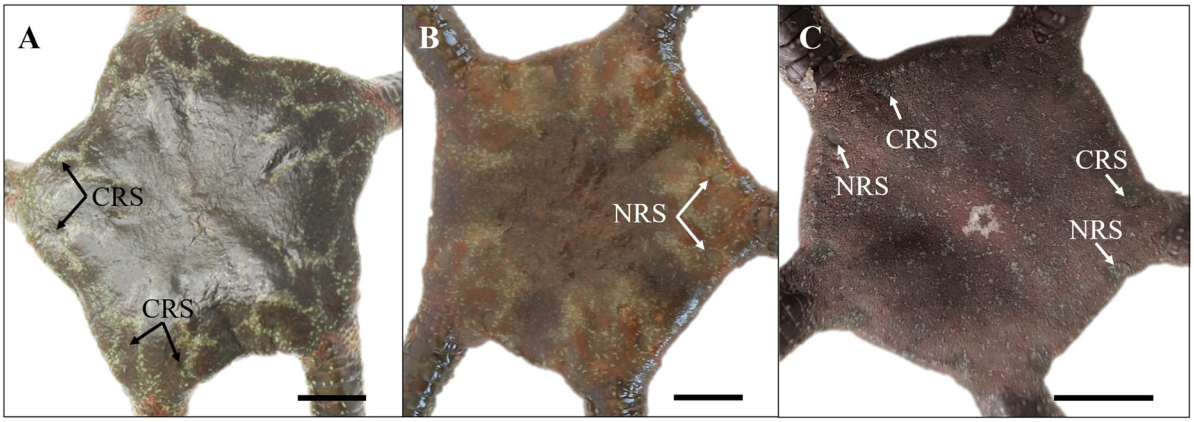

FIGURE 6. Covered (a), naked (b) and mixed (c) radial shield. CRS: Covered Radial Shield. NRS: Naked Radial Shield. Scale bare = 0.5 mm.

Mode of reproduction

The sample consisted of 31 females, 34 males and 2 individuals of undetermined sex. The gonads histology showed b*rooding* and spawning females (Table 5). Brooders female were collected in March (23) at Salamandre and Stidia-East stations. The embryos were at the gastrula stage (Figure 7A, 7B). The spawners females were collected in August and September. They were at partially spawned (Figure 7D), post-spawned (Figure 7E) a nd recovery stages (Figure 7F). During the partially spawned stage, some ova had mature oocytes while others were empty with a few relic oocytes. The ova were mostly empty during the post-spawned stage, with a low production of new oocytes, in others new nutritional cells appeared. The recovery stage was characterized by a high production of new oocytes and an excessive presence of nutritional cells. For the mature stage (Figure 7C), generally the ova were filled with mature oocytes whose diameter was approximately 182.75 ± 20.52 µm.

TABLE 4. Individual morphology of the Ophioderma species from the Algerian west coast. dd : disc diameter, DAP: Dorsal Arm Plates, RS: Radial Shield, AS: Arm Spines, OP: Oral Papillae. The letters (A–U) in the DAP distal edge Column refer to the description in Table 2 and Figure 3. The roman numerals (I–X) in the dorsal colour Column refer to the descriptions in Table 3 and Figure 4. The ventral colour refer to Figure 5. The number of oral papillae is given as an interval, the most frequent number is indicated just after the interval followed by its frequency of appearance between brackets (e.g. individual LPVCMRMS2021.652 had between 7 and 11 papillae and the number 8 occurred five times). The empty cells indicate the same observation as the previous one.

Individual code	dd (mm)	DAP distal edge	Dorsal colour	Ventral colour	DAP type	DAP Thickness	RS	AS number	OP number	Common criteria with *Ophioderma* species
						Salamandre				
LPVCM-RMS2020.601	23.41	U	IX	Light green and cream	Multi-ple / 2 pieces	Flat	Naked	[7–10]	8	7 criteria of *O. hybridum* and 5 of *O. zibrowii*
LPVCM-RMS2020.602	23.67	B	III	As dorsal disc turns to creamy	Multiple	Tumid	Mixed	[9–10]	[7–9] 8	6 criteria of *O. hybridum* and 4 of *O. zibrowii* and *O. longicaudum*
LPVCM-RMS2020.603	25.39	N	IV	Cream yellow to orange		Flat	Naked	[8–9]	[7–8] 8	7 criteria of *O. hybridum*, 4 of *O. zibrowii* and 2 of *O. longicaudum, O. guineense and O. africanum*
LPVCM-RMS2020.604	25.61	A	I	As dorsal disc			Mixed	[8–12]	[8–9] 9	6 criteria of *O. hybridum*, 4 of *O. zibrowii* and 4 of *O. guineense*
LPVCM-RMS2020.605	24.60	B	I				Covered	[7–9]	[7–8]	7 criteria of *O. hybridum*, 3 of *O. guineense* and 2 of *O. longicaudum, O. guineense and O. africa-num*
LPVCM-RMS2020.606	22.07	F	I	Degradation of dark brown to cream				[8–7]	8	7 criteria of *O. hybridum*, 4 of *O. guineense* and 3 of *O. longicaudum*
LPVCM-RMS2020.607	23.91	C	III	As dorsal	Single	Tumid		[7–8]	[8–9]	6 criteria of *O. hybridum* and 2 of *O. zibrowii* and *O. longicaudum*
LPVCM-RMS2020.608	24.71	O	VI	As dorsal but lighter	Multiple	Weakly tumid	Naked	[7–11]	[7–8]	5 criteria of *O. hybridum* and 4 of *O. longicaudum*

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TABLE 4. (Continued)

Individual code	dd (mm)	DAP distal edge	Dorsal colour	Ventral colour	DAP type	DAP Thickness	RS	AS number	OP number	Common criteria with *Ophioderma* species
LPVCM-RMS2020.609	21.68	E	I	As dorsal disc	Single	Flat	Covered	[7–9]	[8–9] 8	6 criteria of *O. hybridum* and 2 of *O. zibrowii* and *O. guineense*
LPVCM-RMS2020.610	22.51	C	I	Olive white spots	Multiple				[8–11] 9	7 criteria of *O. hybridum* and 4 of *O. guineense*
LPVCM-RMS2020.611	25.16	B	I	As dorsal disc		Tumid	Mixed		[8–10] 8	6 criteria of *O. hybridum* and 4 of *O. zibrowii*
LPVCM-RMS2020.612	24.98	L	III	As dorsal disc turns to creamy	Multiple	Flat	Naked	[7–11]	[7–9] 8	6 criteria of *O. hybridum*, 4 of *O. zibrowii* and 3 of *O. guineense*
LPVCM-RMS2020.613	22.77	B	I	As dorsal disc		Tumid	Covered	[7–10]	[7–10] 9	7 criteria of *O. hybridum* and 5 of *O. longicaudum*
LPVCM-RMS2020.614	20.33	B	I	Brown white spots	2 pieces	Flat		[8–10]	[8–9]	9 criteria of *O. hybridum*, 4 of *O. africanum* and 3 of *O. guineense*
LPVCM-RMS2020.615	19.05	A	I	As dorsal disc	Multiple			[7–10]	[7–10]	9 criteria of *O. hybridum*, 4 of *O. longicaudum* and *O. guineense*
LPVCM-RMS2020.616	20.12	H	I	As dorsal disc	Multiple	Flat	Naked	[8–11]	[7–10]	8 criteria of *O. hybridum* and 5 of *O. zibrowii*
						Stidia-West				
LPVCM-RMS2020.617	19.21	A	I	As dorsal disc	Multiple	Tumid	Covered	[7–8]	[7–9]	5 criteria of *O. hybridum* and 4 of *O. longicaudum*

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TABLE 4. (Continued)

Individual code	dd (mm)	DAP distal edge	Dorsal colour	Ventral colour	DAP type	DAP Thickness	RS	AS number	OP number	Common criteria with *Ophioderma* species
LPVCM-RMS2020.618	18.38	Q	VIII	As dorsal disc	2 pieces	Weakly tumid	Naked	[7–10]	8	4 criteria of *O. hybridum* and 5 of *O. longicaudum*
LPVCM-RMS2020.619	19.00	A	I	Brown. white spots	Multiple	Tumid	Mixed		[7–10]	7 criteria of *O. hybridum* and 3 of *O. longicaudum*
LPVCM-RMS2020.620	19.81	B	I	As dorsal disc					8	7 criteria of *O. hybridum* and 4 of *O. longicaudum*
LPVCM-RMS2020.621	18.17	A	II					[8–10]	[7–10] 8	7 criteria of *O. hybridum* and 4 of *O. longicaudum*
LPVCM-RMS2020.622	23.45	N	IV			Flat	Naked	[7–12]	[7–9] 8	5 criteria of *O. hybridum* and 3 of *O. zibrowii*
						Stidia-East				
LPVCM-RMS2021.623	22.05	G	I	As dorsal disc	Multiple	Flat	Naked	[8–12]	[7–9] 8 (6)	7 criteria of *O. hybridum,* 5 of *O. guineense* and 4 of *O. zibrowii*
LPVCM-RMS2021.624	19.51	D	II	As dorsal disc	Multiple	Weakly tumid	Covered	[7–11]	[7–10]	7 criteria of *O. hybridum* and 4 of *O. guineense*
LPVCM-RMS2021.625	22.62	D	I			Weakly tumid		[7–10]	[7–9]	6 criteria of *O. hybridum* and 4 of *O. guineense*
LPVCM-RMS2021.626	22.95	D	I		2 pieces	Flat	Mixed	[8–10]	[7–8] 8	7 criteria of *O. hybridum* and 4 of *O. zibrowii* and *O. guineense*
LPVCM-RMS2021.627	17.83	A	I		Single	Tumid		[8–11]	[7–8]	8 criteria of *O. hybridum* 5 of *O. zibrowii* and 4 of *O. guineense*
LPVCM-RMS2021.628	24.94	D	III		Multiple			[8–10]	[7–8]	8 criteria of *O. hybridum* and 4 of *O. zibrowii*

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TABLE 4. (Continued)

Individual code	dd (mm)	DAP distal edge	Dorsal colour	Ventral colour	DAP type	DAP Thickness	RS	AS number	OP number	Common criteria with *Ophioderma* species
LPVCM-RMS2021.629	22.53	B	III	As dorsal disc	Multiple	Tumid	Naked	[7–9]	[8–10] 8	6 criteria of *O. hybridum* and 5 of *O. zibrowii* and *O. longicaudum*
LPVCM-RMS2021.630	22.00	N	V					[7–10]	[8–10] 9 (7)	8 criteria of *O. hybridum* and 5 of *O. longicaudum*
LPVCM-RMS2021.631	24.49	A	I		2 pieces		Mixed	[7–10]	[7–10] 8 (6)	7 criteria of *O. hybridum* and 3 of *O. longicaudum*
LPVCM-RMS2021.632	20.84	M	VIII		Multiple	Flat	Covered		[5–9] 8 (7)	6 criteria of *O. hybridum* and 3 of *O. longicaudum, O. guineense, O. africanum and O. zibrowii*
LPVCM-RMS2021.633	20.77	B	I				Mixed		[7–9] 8 (5)	7 criteria of *O. hybridum* and 2 of *O. longicaudum, O. guineense, O. africanum and O. zibrowii*
LPVCM-RMS2021.634	19.15	S	VIII		Single	Tumid	Naked	[7–12]	[7–9] 8 (5)	6 criteria of *O. hybridum* and 3 of *O. zibrowii*
LPVCM-RMS2021.635	14.58	Q	VIII				Covered	[7–9]	[7–8] 8 (9)	6 criteria of *O. hybridum* and 3 of *O. guineense* and *O. longicaudum*
LPVCM-RMS2021.636	21.27	U	X		Multiple	Flat	Naked	[7–10]	[7–9] 8 (6)	8 criteria of *O. hybridum*, 3 of *O. guineense* and 2 of *O. longicaudum, O. africanum and O. zibrowii*

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TABLE 4. (Continued)

Individual code	dd (mm)	DAP distal edge	Dorsal colour	Ventral colour	DAP type	DAP Thickness	RS	AS number	OP number	Common criteria with *Ophioderma* species
LPVCM-RMS2021.637	23.12	A	I	As dorsal disc	2 pieces	Weakly tumid	Mixed	[8–10]	[7–9]	7 criteria of *O. hybridum* and 4 of *O. zibrowii*
LPVCM-RMS2021.638	23.35	A	II		Multiple	Tumid		[8–11]	8	5 criteria of *O. longicaudum* and 5 of *O. hybridum*
LPVCM-RMS2021.639	24.22	P	VII			Weakly tumid	Covered	[8–11]	[7–9] 8 (7)	5 criteria of *O. hybridum* and 4 of *O. longicaudum*
LPVCM-RMS2021.640	26.66	B	III			Tumid	Naked	[8–11]	[7–10] 8 (4)	5 criteria of *O. hybridum* and 3 of *O. zibrowii* and *O. longicaudum*
LPVCM-RMS2021.641	21.74	B	III		2 pieces		Covered	[8–12]	[8–9]	6 criteria of *O. hybridum* and 4 of *O. guineense* and *O. longicaudum*
LPVCM-RMS2021.642	20.36	B	I			Flat	Naked	[7–10]	[8–10] 8 (7)	8 criteria of *O. hybridum* and 7 of *O. zibrowii*
LPVCM-RMS2021.643	17.73	A	I				Covered	[7–11]	[8–10] 9 (6)	6 criteria of *O. hybridum*, 5 of *O. guineense* and 4 of *O. zibrowii*
LPVCM-RMS2021.644	19.85	M	III				Mixed	[8–10]	[7–9] 8 (6)	7 criteria of *O. hybridum* and 5 of *O. zibrowii*
LPVCM-RMS2021.645	23.22	A	I			Weakly tumid	Covered	[7–10]	[8–10] 9 (6)	7 criteria of *O. hybridum* and 3 of *O. guineense*
LPVCM-RMS2021.646	19.79	A	I		Multiple		Mixed	[7–11]	[7–9] 8 (5)	5 criteria of *O. hybridum* and 3 of O. *zibrowii*
LPVCM-RMS2021.647	14.41	M	VIII			Flat	Covered	[7–9]	[7–10] 8 (5)	8 criteria of *O. hybridum* and 4 of *O. guineense*

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TABLE 4. (Continued)

Individual code	dd (mm)	DAP distal edge	Dorsal colour	Ventral colour	DAP type	DAP Thickness	RS	AS number	OP number	Common criteria with *Ophioderma* species
LPVCM-RMS2021.648	24.41	I	I	As dorsal disc	2 pieces	Weakly tumid	Mixed	[7–10]	[8–11] 8 (6)	5 criteria of *O. hybridum*, 2 of *O. africanum* and 3 of *O. longicaudum*
LPVCM-RMS2021.649	23.41	J	I					[8–12]	[6–9] 8 (5)	5 criteria of *O. hybridum*, 3 of *O. zibrowii* and 1 of *O. longicaudum*
LPVCM-RMS2021.650	25.43	A	I				Covered	[8–13]	[8–10] 8 (5)	5 criteria of *O. hybridum* and 2 of *O. guineense* and *O. africanum*
LPVCM-RMS2021.651	23.66	A	I				Mixed	[8–11]	[7–9] 8 (5)	6 criteria of *O. hybridum* and 3 of *O. zibrowii*
LPVCM-RMS2021.652	25.20	A	I		Multiple	Tumid		[8–10]	[7–11] 8 (5)	6 criteria of *O. hybridum*, 4 of *O. zibrowii* and 1 of *O. longicaudum*
LPVCM-RMS2021.653	21.26	B	I			Weakly tumid			[7–9] 7 (5)	7 criteria of *O. hybridum* and 4 of *O. zibrowii*
LPVCM-RMS2021.654	22.62	B	I		2 pieces	Flat		[7–10]	[7–9] 8 (5)	7 criteria of *O. hybridum*, 5 of *O. zibrowii* and 1 of *O. longicaudum*
LPVCM-RMS2021.655	18.93	A	I		Multiple			[8–10]	[7–10] 8 (5)	7 criteria of *O. hybridum* and 4 *O. zibrowii*
LPVCM-RMS2021.656	17.01	K	I		Single	Tumid		[7–10]	[7–8] 7 (7)	6 criteria of *O. hybridum*, 4 of *O. zibrowii* and 1 of *O. longicaudum*
LPVCM-RMS2021.657	15.27	K	I		Single	Flat	Covered	[7–8]	[7–8] 8 (8)	7 criteria of *O. hybridum* and 4 of *O. zibrowii* and *O. guineense*
LPVCM-RMS2021.658	21.03	A	I		2 pieces		Mixed	[9–11]	[7–10] 8 (8)	6 criteria of *O. hybridum*. 4 of *O. zibrowii* and 4 of *O*. guineense

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TABLE 4. (Continued)

Individual code	dd (mm)	DAP distal edge	Dorsal colour	Ventral colour	DAP type	DAP Thickness	RS	AS number	OP number	Common criteria with *Ophioderma* species
LPVCM-RMS2021.659	14.17	A	I	As dorsal disc	Multiple	Weakly tumid	Covered	[7–9]	[7–9] 8 (5)	7 criteria of *O. hybridum* and 2 of *O. longicaudum, O. guineense, O. africanum and O. zibrowii*
LPVCM-RMS2021.660	24.91	B	I			Tumid	Mixed	[8–11]	[13–9] 9(4)/10(4)	4 criteria of *O. hybridum* and 3 of *O. zibrowii*
LPVCM-RMS2021.661	25.95	B	II		2 pieces		Naked	[8–11]	[7–8]	4 criteria of *O. hybridum*, 3 of *O. zibrowii* and 2 of *O. longicaudum*
LPVCM-RMS2021.662	23.49	B	III		Multiple		Covered	[7–10]	[7–10] 8 (4)	7 criteria of *O. longicaudum* and 6 of *O. hybridum*
LPVCM-RMS2021.663	22.58	A	II		2 pieces	Weakly tumid	Mixed	[7–11]	[8–9] 9 (8)	6 criteria of *O. hybridum* and 2 of *O. longicaudum*
LPVCM-RMS2021.664	21.91	R	VIII			Flat	Naked	[7–10]	[7–9] 9 (5)	6 criteria of *O. hybridum* and 2 of *O. zibrowii* and *O. africanum*
LPVCM-RMS2021.665	19.14	S	VIII	As dorsal with orange pattern on disc			Mixed		[7–9] 8 (5)	6 criteria of *O. hybridum* and 3 of *O. africanum*
LPVCM-RMS2021.666	16.75	A	II	As dorsal disc		Weakly tumid	Covered		[7–9] 8/9 (4)	7 criteria of *O. hybridum*, 4 of *O. africanum* and 3 of *O. guineense*
LPVCM-RMS2021.667	21.29	T	VIII	As dorsal with orange pattern on disc	Multiple	Flat	Covered	[8–10]	[7–10] 8(5)	7 criteria of *O. hybridum* and 5 of *O. longicaudum*

TABLE 5. Reproduction mode of females collected in March, May, June, August and September.

Individual	Period	location	Sexual maturity stage	Reproduction mode
LPVCMRMS2020.614	March	Salamandre	Mature	Brooding
LPVCMRMS2020.615			Gastrula	
LPVCMRMS2020.616			Gastrula	
LPVCMRMS2021.625		Stidia-East	Maturity	Undefined
LPVCMRMS2021.627			Mature	Brooding
LPVCMRMS2021.630				
LPVCMRMS2021.633				
LPVCMRMS2021.636	May			
LPVCMRMS2021.638	Jun			
LPVCMRMS2021.642				
LPVCMRMS2021.649	August		Partially spawned	Spawning
LPVCMRMS2021.652				
LPVCMRMS2021.654			Mature	
LPVCMRMS2021.656				
LPVCMRMS2021.658			Partially spawned	
LPVCMRMS2021.660	September		Recovery	Undefined
LPVCMRMS2021.662			Post-spawning	Spawning
LPVCMRMS2021.663			Partially spawned	
LPVCMRMS2021.664			Recovery	Undefined

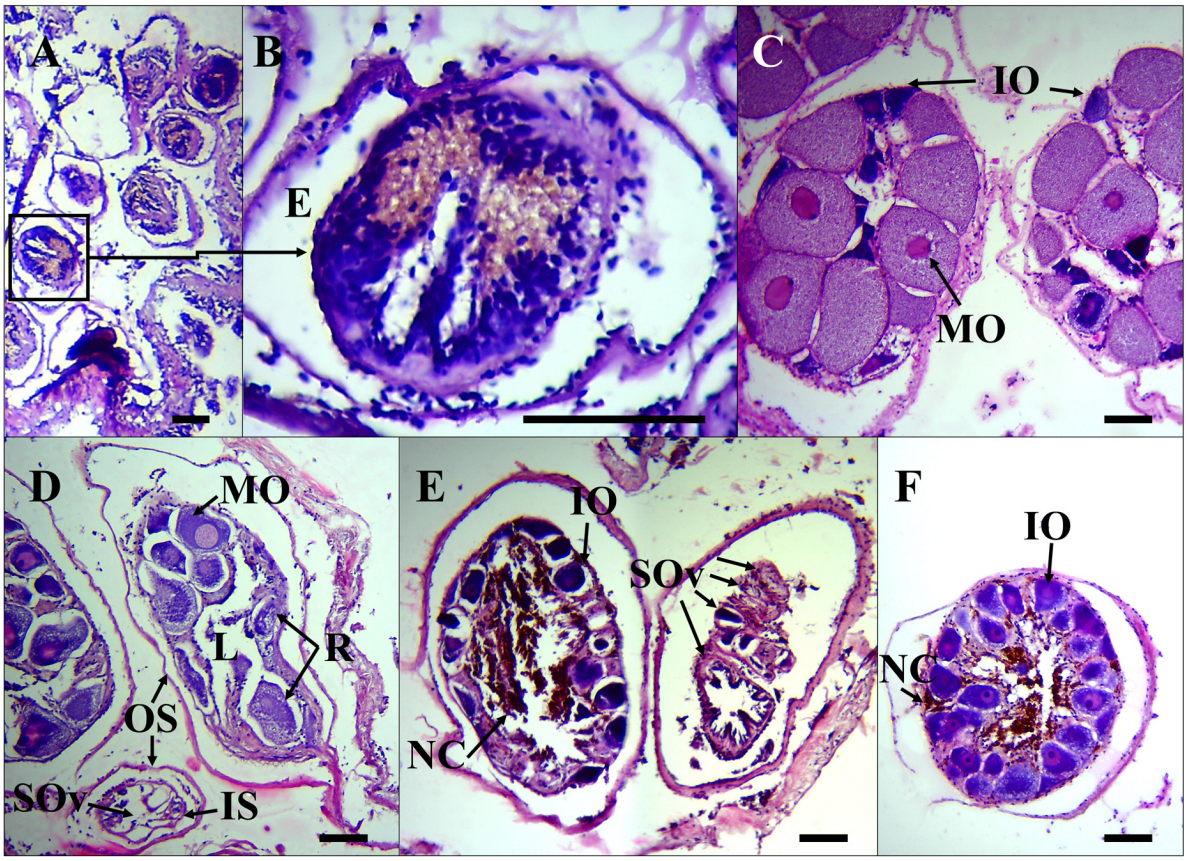

FIGURE 7. Photomicrograph of *Ophioderma* female gonads. A: overview of brooding gonads. B: Embryo at the gastrula stage. C: ovary at mature stage. D: partially spawned stage. E: post-spawned stage. F: recovery stage. E: Embryo, IO: Immature Oocyte, MO: Mature Oocyte, OS: Outer Sac, IS: Inner Sac, L: Luman, R: Relic, SOv: Spent Ovary, NC: Nutritional Cells. Scale bar = 100 µm.

Morphometric analysis

The Canonical Variates Analysis showed a significant discrimination between the three stations (λ-Wilk = 0.2402, *p-value* = 6.955 E-10, Figure 8A, Table 6). Indeed, there is a station effect defined by several variables sloped on the first axis (61.39%; Figure 8B), namely arm length, arm width, madreporite length and width, madreporite ratio, oral shield width, the presence or absence of white spots on the ventral arm plates (Figure 2B) and interraduis width. On the second axis (38.61 %; Figure 8B), oral shield length and adoral shield length were projected. The variables showed a size gradient that decreases towards the west of the Mostaganem coast. Individuals collected from Salamandre were the largest, those from Stidia-East had an intermediate size and those from Stidia-West were the smallest.

TABLE 6. Canonical Variates Analysis Post hoc test (*p-values*) results obtained on the morphometric differences between individuals of the Algerian west coast species of *Ophioderma* among sampling localities.

	Salamandre	**Stidia-West**	**Stidia-East**
Salamandre		0.01	9.96 E-06
Stidia-West	0.01		0.0001
Stidia-East	9.96 E-06	0.0001	

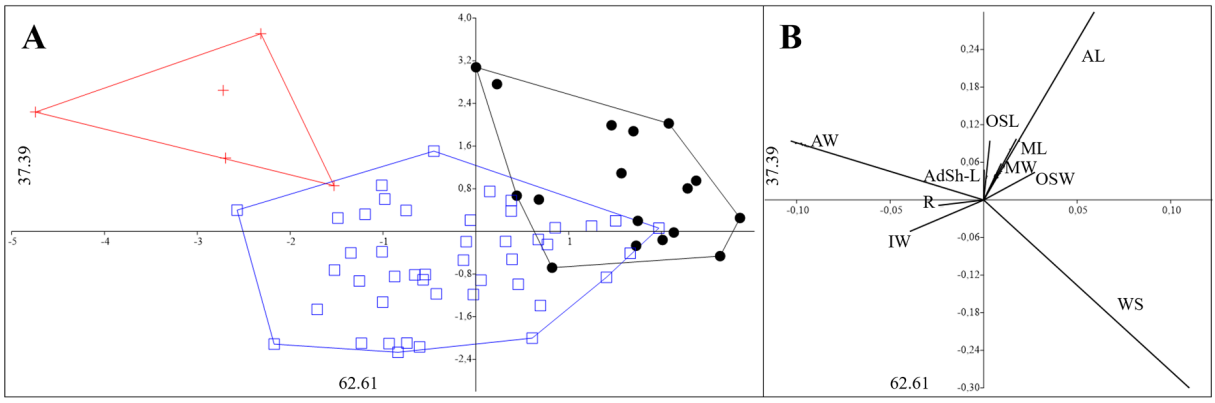

FIGURE 8. Canonical variates analysis scatter plot (A) and parameters used (B) in the morphometric study of *Ophioderma* species collected from Salamndre (●), Stidia-East (□) and Stidia-West (+). AL: Arm Length, AW: Arm Width, ML: Madreporite Length, MW: Madreporite Width, R: Madreporite Ratio, OSL: Oral Shield Length, OSW: Oral Shield Width, WS: the presence or absence of white spots on the ventral arm plates IW: Interraduis Width, AdSh-L: Adoral Shield Length.

Salamandre individuals had long and thin arms separated by a small distance (interradius width) with an imporant oral shield, madreporite and adoral shield. On the other hand, individuals from Stidia-East had short and thick arms, separated by a large distance (interradius width), madreporite, oral shield and adoral shield had small size. The individuals from Stidia-West were in the middle, but some shared the same characteristics with those from Stidia-East and others with those from Salamandre. The ventral arm plates of 20 individuals collected from Stidia-East and six individuals from Salamandre tended to be mottled in contrast to those from Stidia-West.

Discussion

The studied sample of *Ophioderma* species showed a huge morphological variability. Most individuals (five from Stidia-West, 13 from Salamandre and 43 from Stidia-East) had between five and nine character states in common with *O. hybridum*. Nevertheless, they shared some similarities with: 1. *O. longicaudum* mainly by the red pigmentation, multiplications and thickness of the dorsal arm plates, 2. *O. zibrowii* by the naked radial shield, 3. *O. africanum* by the black spots on the distal edge of the dorsal arm plates, thickness and multiplications of the latter and 4. *O. guineense* by the cream-coloured ventral disc, colour and multiplications of the dorsal arm plates.

Morphological criteria overlaped mainly between *O. hybridum* and *O. zibrowii* in Salamandre individuals, *O. hybridum* and *O. longicaudum* in Stidia-West individuals and between the three aforementioned species in Stidia East individuals, but they overlaped rarely with *O. guineense* and *O. africanum* (Table 4). We can therefore note that our sample consistsed mainly of *O. hybridum*, *O. longicaudum* and *O. zibrowii*. In addition to morphological criteria, this finding could be supported by other factors such as the geographical distance between the distribution areas and the collection depths of the different species. In fact, the first three species (*O. hybridum*, *O. longicaudum* and *O. zibrowii*) were found in the Mediterranean Sea (France, Tunisia and Greece) in shallow waters, while the other two (*O.* guineense and *O. africanum*) were present in West Africa (Sao Tomé and Rolas Islands, Gulf of Guinea, Equatorial Guinea and Senegal) in deeper waters (Stöhr *et al.* 2009; Boissin *et al.* 2011; Weber *et al.* 2013, 2014, 2019; Stöhr *et al.* 2020).

Although, the sample was similar to the three species mentioned above, we eliminated *O. zibrowii* because the latter was detected in the Levant Sea where it adapted to its ecological conditions (Stöhr *et al.* 2009, 2012; Weber *et al.* 2014). Generally, the brooders among the species of *Ophioderma* are known in the eastern Mediterranean basin, the Tunisian coast and the southern Aegean Sea, while spawners are mainly found on the French and Croatian coasts (Stöhr *et al.* 2009, 2020). Brooding in these species is considered as an adaptation to the low nutrient content of their environment (Stöhr *et al.* 2009, 2020). Nevertheless, the authors were able to record the presence of both brooders and spawners at the same time in Cyprus and Lebanon.

The individuals showed considerable morphological variations, with new characteristics, which were not shown in the previous studies such as the higher number of oral papillae and arm spines reported in large individuals. According to Stöhr *et al.* (2020), this high variability was very noticeable for *O. hybridum*. The authors suggested that this species is an ancient hybrid of *O. longicaudum* and *O. zibrowii*, hence, it shares several traits with its two ancestral species, leading us to suppose that the majority of the studied individuals may belong to *O. hybridum*. Individuals LPVCMRMS2021.638 and LPVCMRMS2021.662 had between five and six criteria in common with *O. longicaudum*. The remaining individuals (LPVCMRMS2020.618, LPVCMRMS2021.660 and LPVCMRMS2021.661) had fewer criteria in common with all *Ophioderma* species and possessed criteria that did not resemble any of the five species listed above (Table 4).

Knowledge of the species ecology is a valuable tool in integrative taxonomy (Borojević 1967; Beauchard *et al.* 2017; Chenuil *et al.* 2019) such as nature of the substratum. This factor may influence the distribution of different species or even different lineages of the same species such as the sand burrowing brittle stars *Acrocnida brachiata* (Montagu, 1804), where adult migration favoured the appearance of a new haplotype (Muths 2006) which was then split into two species *A. brachiata* and *A. spatulispina* (Stöhr & Muths 2010). But this tool did not seem to be very useful in this case, because the species of *Ophioderma* in our study and those of Stöhr *et al.* (2009), Boissin *et al.* (2011), Stöhr *et al.* (2020) showed a preference for rocky habitats under or/and between rocks and cliffs (Table 1). This preference may be due to the negative phototactic of these species (Hendler *et al.* 1995).

The mode and period of reproduction are criteria that can only be used for a short period. Our sample consists of brooders and spawners collected from Salamandre and Stidia-East. This did not exclude the presence of both in Stidia-West but we did not collect during the reproduction season in this area. We detected embryos at the gastrula stage in March which means that the fecundation was carried out some days before. Weber *et al.* (2014) detected embryos of *O. zibrowii* at the same stage in May in the eastern Mediterranean. It is well known that brooding is the mode of reproduction of *O. hybridum*, but its period of reproduction is undetermined until now (Stöhr *et al.* 2020), this could mean that our individuals belong to *O. hybridum* and the period of reproduction of the latter could occur in March/April in the Western Mediterranean, exactly on the Algerian west coast. The spawners were collected between August and September which overlaped with the reproduction period of *O. longicaudum* and *O. africanum*, but for the reasons given above we can conclude that they were *O. longicaudum*.

The morphometric study reveals a difference in size between stations, the individuals collected from Salamandre were the largest, those from Stidia-East had an intermediate size and those from Stidia-West were the smallest the individuals. Previous studies on the Mediterranean/West African species of *Ophioderma* confirmed that spawners such as *O. longicaudum* had a larger disc diameter compared to brooders such as *O. hybridum* (Stöhr *et al.* 2009; Weber *et al.* 2014).

The mottled aspect of the ventral arm plates was very noticeable in individuals collected from Stidia-East, this may be due to the large number of individuals collected from this site compared to the others.

In general, the results obtained by both morphological and morphometric methods are similar for most

individuals studied, which means that individuals who had more or less the same morphological criteria had the same dimensional characteristics, which supports our findings on their grouping and identification. Morphological variability of our sample indicates the existence of at least two species (*O. longicaudum* and *O. hybridum*) inhabiting a very restricted area (from a few meters to several kilometres). Thus, we suppose that they can even inhabit the same biotope.

Conclusion

In Algeria, studies on the *Ophioderma* species are almost non-existent. This study constitutes a first approach to brittlestar biodiversity at the western Algerian coast and Alboran Sea. The result obtained shows that the studied individuals appear to belong to two species, namely *O. hybridum* and *O. longicaudum*. Although, the morphological study, which is considered as the most accessible method to delimit the species boundaries, is not sufficient to formally identify the individuals. Therefore, it is important to explore other fields such as molecular biology and ecology, in particular their diet and their ecological niches, as well as their reproduction mode, given the possibility of cohabitation of these species in the same biotope.

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