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Range extension and morphological variability of Ophioderma longicaudum (Echinodermata: Ophiuroidea) at the South-West Atlantic coast of France

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Abstract :

Specimens of the brittle star genus Ophioderma were found at the South-West Atlantic coast of France. They were sampled between 2 and 40 m depth. Morphologically, these specimens were most similar to O. longicaudum and O. hybridum. Molecular analysis for a mitochondrial marker (COI) and nuclear marker EF1 sequences from twelve specimens showed that only O. longicaudum was present in this study, with a higher morphological variability than previously described. They represent the northernmost confirmed record for this species, yet.

Résumé :

Extension de l'aire de répartition et variabilité morphologique d'Ophioderma longicaudum (Echinodermata : Ophiuroidea) sur la côte atlantique sud-ouest de la France. Des spécimens du genre Ophioderma ont été récoltés sur la côte Atlantique Sud-Ouest de la France. Ils ont été échantillonnés entre 2 et 40 m de profondeur. Morphologiquement, ces spécimens ressemblaient le plus à O. longicaudum et O. hybridum. L'analyse moléculaire des séquences d'un marqueur mitochondrial (COI) et d'un marqueur nucléaire EF1 provenant de douze spécimens a montré que seul O. longicaudum était

présent dans cette étude, avec une variabilité morphologique plus élevée que celle décrite précédemment. Il s'agit à ce jour du signalement confirmé le plus septentrional pour cette espèce.

Keywords : Bay of Biscay, Saint-Jean-de-Luz, Arcachon Bay, Morphology, DNA, New records

Introduction

Taxonomic and ecological work provides a better knowledge of species, with the aim of better understanding the functioning of ecosystems and geographical distribution of a species, but also to obtain more reliable data on the species richness in an area or habitat. Sometimes changes in species occurrences (increase, decrease, displacement) can be linked to climate change or human activities (for non-indigenous species). In some cases, further studies allow to highlight the existence of species complexes, with the description of new species (Bannar-Martin et al., 2018; Stöhr et al., 2020; Kamcha et al., 2023)

Ophioderma longicaudum (Bruzelius, 1805), the type species of its genus, was originally described from the Mediterranean Sea. In 2009, Stöhr et al., began to launch the idea of a cryptic species complex due to differences in reproduction (broadcast spawning vs. brooding) between some Mediterranean populations. Genetic analyses suggested the existence of at least two different species (Boissin et al., 2011; Weber et al., 2014 & 2015), and later up to six species in the Mediterranean Sea and North-East Atlantic Ocean (Weber et al., 2019). Stöhr et al. (2020) resolved the *O. longicaudum* cryptic species complex by describing three new species, with a potential fourth, thus increasing the number of species of *Ophioderma* in European waters from one to three (*O. longicaudum*, *O. zibrowii* Stöhr, Weber, Boissin & Chenuil, 2020, and *O. hybridum* Stöhr, Weber, Boissin & Chenuil, 2020). In addition, two species were confirmed off West Africa (*O. guineense* Greef, 1882, *O. africanum* Stöhr, Weber, Boissin & Chenuil, 2020). Although the species delimitations rested mainly on genetic data, morphological differences were recognized and described (Stöhr et al., 2020). So far, the northernmost limit of the known distribution of *O. longicaudum* identified by genetic analyzes in the eastern Atlantic was off the southern tip of Portugal (Stöhr et al., 2020), at subtidal depths. Intertidal specimens have been recorded at the Basque coast, but identification was based only on morphological characters and does not correspond to the known bathymetric distribution of *O. longicaudum* (de Casamajor et al., 2017; Huguenin et al., 2018). The CIRCATAX (CIRCAlitoral TAXonomy) project aims to determine the biodiversity of caves, drop-offs, and overhangs in an area of the French Basque coast in two stations: “Gruyere” and “Gorgone” (Fig. 1). Sampling was carried out in 2020 and 2021 between 16 and 40 m depth. These collection efforts have found specimens of *Ophioderma*, and therefore outside the known limit of distribution. The specimens displayed a range of morphological features and colour patterns, resembling both *O. longicaudum* and *O. hybridum*. This suggests the presence of either both species or a single species exhibiting significant morphological variability. However, this determination could not be made solely based on morphology. The present study had a dual purpose. Firstly, we sequenced two genetic markers from specimens collected in 2022, which were selected from the previously utilized genetic markers (Weber et al., 2019) to validate the species identification. Secondly, we documented the range and the morphological variability of the species.

Material and Methods

Genetic analyses and morphological characters herein presented were based on *Ophioderma* specimens collected in July 2022 at two stations in French Basque Coast: station “St_1”, 8 m depth, specimens numbers 1 to 8, 43°24.620”N, 1°38.751”W; station “St_2”, 5 m depth, specimens numbers 9 to 16, 43°23.241”N, 1°43.246”W; and in July 2023 at one station in Arcachon Bay: station “Arcachon”, 2 m depth, specimens numbers 17 and 18, 44°39.898”N, 1°9.818”O (Fig. 1). They were preserved in 80% alcohol, examined with a Nikon SMZ 25 stereomicroscope equipped with NIS-Elements Analysis software for pictures. Some specimens were deposited at the Muséum National d’Histoire Naturelle (MNHN) of Paris, France (Supplementary material Table 1).

We attempted to sequence two genetic markers in all specimens. These markers were chosen, because in the previous studies, for the COI marker, haplotypes (i.e. nucleotide sequence variants) of each cryptic species formed a monophyletic group well separated from other species haplogroups (reciprocal monophyly) (Fig. 2). *Ophioderma longicaudum* haplotypes differed from *O. africanum* and from *O. zibrowii* by ca. 14 nucleotide differences, and even more with *O. guineense*. The nuclear marker distinguishes three groups of species: (i) *O. guineense* (also known as Cluster C1), (ii) *O. zibrowii* (Clusters C5-C6) and (iii) *O. longicaudum* (Cluster C3), *O. africanum* (Cluster C2) and *O. hybridum* (Cluster C4) with these three species sharing identical allele sequences. DNA was extracted using the Qiagen ‘DNeasy blood and tissue kit’, from pieces of arms conserved in ethanol at room temperature after specimen collection. DNA was eluted twice in 200µL from the kit’s column. We directly used 2 µL of this extract in Polymerase Chain Reaction (PCR) for all specimens. In addition, to increase chances in PCR success, we used DNA extracts diluted 10 times (for specimens 1-2-4-5-7-9-11 those for which the

Figure 1. *Ophioderma longicaudum* (Bruzelius, 1805). Sampling stations. Gr: Gruyere, Go: Gorgone. Scale bar: 2.5 km.

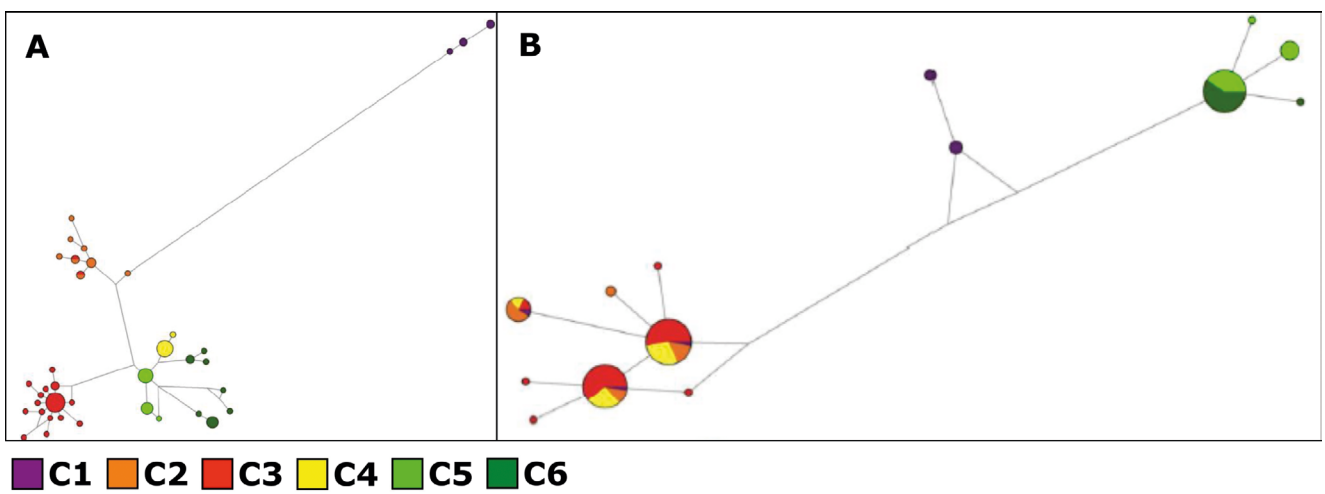

Figure 2. Haplotype networks (extracted from the supplementary information in Weber et al., 2019) for the two genetic markers sequenced. **A.** mitochondrial cytochorme oxidase subunit 1; **B.** nuclear EF1-alpha intron. Each circle represents a haplotype, which size corresponds to the number of specimens. Clusters C1 to C6 corresponded to distinct genetic groups, defined from multilocus genotypes at ~30 markers. Most of these groups were genetically not overlapping even when specimens were found in sympatry suggesting they belonged to non interbreeding entities, thus biological species. Stohr et al (2020) assigned species names to some clusters: C1: *Ophioderma guineense*. C2: *O. africanum*. C3: *O. longicaudum*. C4: *O. africanum*. C5-C6: *O. zibrowii*. To understand the evolutionary scale, consider that one nucleotide difference corresponds to the smallest distance between a central haplotype and a satellite one (generally a singleton, thus a small circle), two or more substitutions correspond to longer branches.

Table 1. *Ophioderma.* Depth distribution species from previous publications and the collection at the Swedish Museum of Natural History (SMNH). Original depths were recorded in ranges, not the precise depth for each individual.

Species	1-3 m	3-10 m	10-30 m	
Ophioderma longicaudum	15	60	-	Weber et al. (2014)
Ophioderma zibrowii	157	48	-	Weber et al. (2014)
Ophioderma longicaudum	51	286	205	Collection SMNH, Stöhr et al (2009 & 2020)
Ophioderma zibrowii	1	108	0	Collection SMNH, Stöhr et al. (2009 & 2020)
Ophioderma hybridum	15	8	0	Collection SMNH, Stöhr et al. (2020)

4 µL of DNA run in an agarose gel were visible after ethidium bromide staining). PCR was performed for two markers, a portion of the mitochondrial cytochrome c oxidase I gene (COI) and a portion of contig 98699 with PCR oligonucleotides defined in table S2 of Weber et al., (2019) which sequence corresponds to a portion of an elongation factor gene, *EF1*. PCR was done in 25 µL with 1.5 mM of $MgCl_{2,}$ 0.2 mM of dNTP, 10 µM of each oligonucleotide, and with 0.65 units of the Promega Go-Taq polymerase. The cycling program was 5 sec. at 94°C followed by 40 cycles of 45 sec. at 94°C, 45 sec. at 50°C, 1 min. at 72°C. PCR products that were visible on an agarose gel were then sent for Sanger sequencing to industry from both sides (with each PCR oligonucleotide) for both markers.

Results

Few specimens collected up to 40 m depth in 2020 and 2021 present typical characters (Fig. 3) of *O. longicaudum*, such as multiple tumid proximal dorsal arm plates, usually 7 or 8 arm spines, up to eight oral papillae, dorsal disc uniformly brown, radial shields covered by granules, dorsal arms uniformly brown or weakly banded, ventral disc of the same colour as the dorsal disc. All the other specimens collected for genetic analyses in 2022, present variable characteristics (Supplementary material Table 1): dorsal arm plates with two or more pieces on the proximal arms segments, single in the smallest specimens (specimen 8 , Fig. 4.8) and up to 4 pieces in the largest (specimen 18), disc brown or olive dorsally

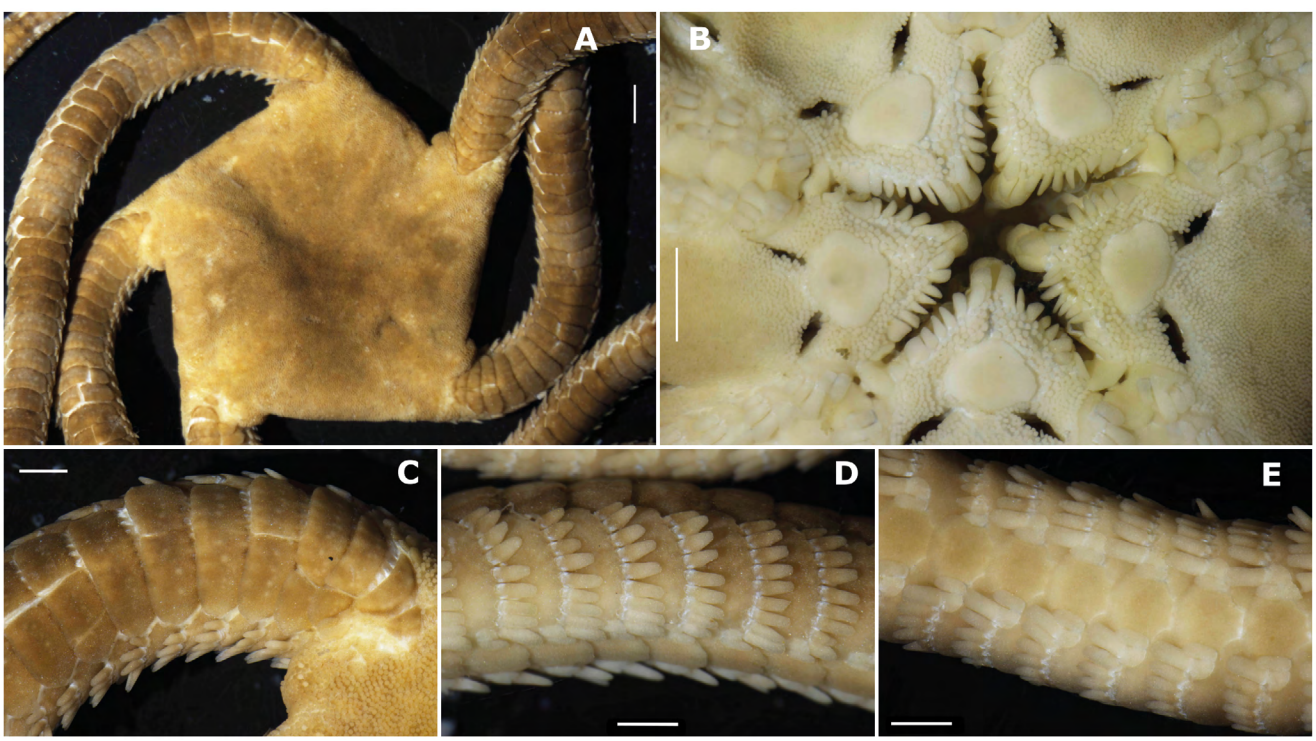

Figure 3. *Ophioderma longicaudum* (Bruzelius, 1805). Typical morphology. Specimen collected on 10 September 2020, station "Gruyere". **A.** Dorsal disc and arm bases. **B.** Mouth. **C.** Dorsal arm. **D.** Lateral arm. **E.** Ventral arm. Scale bars: A & B. 2 mm; C - E: 1 mm.

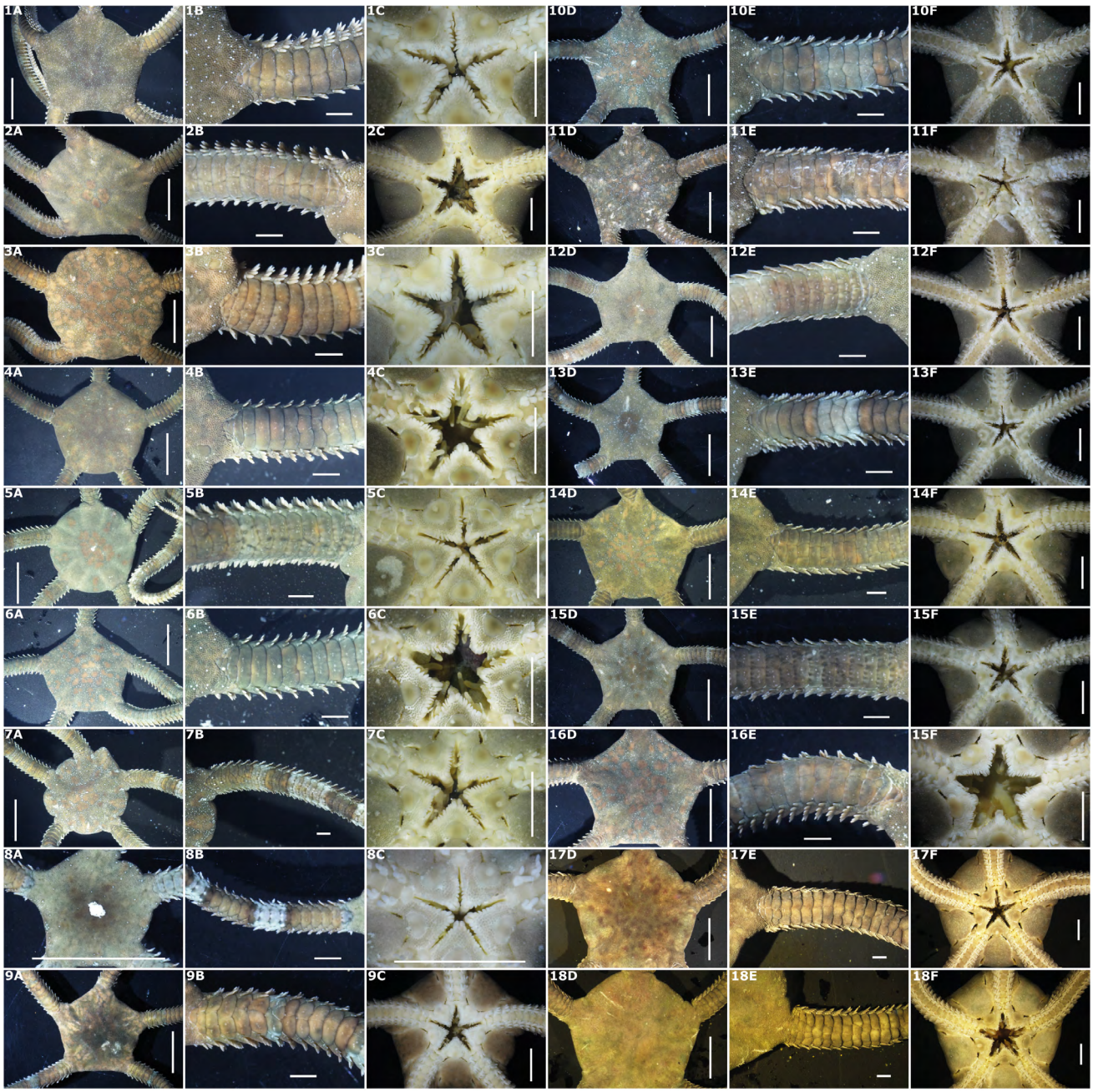

Figure 4. *Ophioderma longicaudum* (Bruzelius, 1805). Colour variations in specimens collected on 08 July 2022 from the French Basque Coast and on 30 July 2022 from Arcachon. 1-18: specimens 1 - 18. Columns A & D show dorsal disc; B & E dorsal arm; C & F ventral disc. Scale bars: Columns A & D: 10 mm; Columns B & E: 2 mm; Columns C & F: 5 mm.

and ventrally, rarely with white spots, radial shields sometimes not covered by granules (Supplementary material Table 1), dorsal arms dark brown (often banded) sometimes with light brown or diffuse white and black spots (Fig. 4). This variability in characters is similar to *O. hybridum* than *O. longicaudum*. Some specimens collected in June 2021 presented immature condition of the gonads whereas some specimens collected in September 2021 presented spent gonads.

Twelve of the eighteen specimens were successfully sequenced for the mitochondrial marker COI and the EF1 marker (all sequenced from forward and reverse directions). For COI, there was a high diversity with 8 distinct haplotypes found for only 12 specimens, but all of them belonged to the same haplogroup that had until now only been found in *Ophioderma longicaudum* (Cluster C3, mitochondrial lineage L1) (Supplementary material Table 1) based on results of

Weber et al. (2019) (see their Fig. S1 for haplotype networks). One of these haplotypes was new but it was linked to various already known haplotypes by a single mutation, thus it did not diverge more than any other haplotype from the group. For the nuclear marker, the twelve specimens successfully sequenced had two alleles separated by a single mutation, both already known and found exclusively in *O. longicaudum, O. hybridum* and *O. africanum*.

Discussion

Based solely on morphological characters and referring to Stöhr et al. (2020), the present specimens would likely have been identified as *O. hybridum,* and potentially extended the geographic range of *O. hybridum* to the French Atlantic coast. Until now, this species was described from Tunisia, and it was only found there, although recently described Algerian populations of *Ophioderma* from the Alboran Sea (the Mediterranean region closest to the Atlantic ocean) (Lebouazda et al., 2022) showed an important morphological variability, that overlapped with *O. hybridum* morphological characteristics, and supposedly included brooding individuals (Lebouazda et al., 2022).

However, genetic analyses, based on previous species delimitation approaches (Weber et al. 2019; Stöhr et al 2020), strongly suggest that these specimens belong to *O. longicaudum*, and thus that this species shows greater morphological variability than previously known.

The molecular analysis identified twelve specimens as *O. longicaudum* and six others could not be assigned due to unsuccessful PCR amplification. *Ophioderma hybridum* was hitherto considered the most variable of the five species in the previous *O. longicaudum* complex, overlapping in the number of arm spines, dorsal arm plates and oral papillae and colour pattern with each of the other four species (Stöhr et al., 2020). *Ophioderma longicaudum* varies in the number of arm spines and oral papillae, but was thought to be less variable in colour, rarely having light spots on disc and arms (Stöhr et al., 2009). Species identification is complicated by age related differences. Numbers of spines, papillae and arm plates vary by size, with smaller specimens tending to have fewer, but there is some variability (Stöhr et al., 2020; Lebouazda et al., 2022). The number of dorsal arm plates is correlated with size as could be seen in the present specimens (Supplementary material Table 1), probably because a fragmentation process may be involved or multiple plates may be the result of injuries accumulating during an animal's life time (Stöhr et al., 2020). *Ophioderma* species appear to be long-lived: Hendler (1991) mentioned that *O. longicaudum sensu lato* may reach a maximum age of 30 years. Stancyk (1974) found *O. brevispinum* (Say, 1825) to be slow growing, taking about nine years to reach 6 mm in disc diameter and an estimated life span of 25-28 years, reproducing for the first time at 2-3 years and 3.9-6.6 mm size. Somatic growth slows down in favour of gonad growth when sexual maturity is reached and there is little somatic growth in winter in *O. brevispinum* (Stancyk, 1974). The neotype of *O. longicaudum* had a disc diameter of 22.5 mm and consequently may be more than 20 years old, which could account for its high number of dorsal arm plates. *Ophioderma hybridum* is assumed to reproduce by brooding and its sister species *O. zibrowii* reproduces in spring (Stöhr et al., 2020), whereas *O. longicaudum* spawns in summer (Fenaux, 1972). The immature condition of the gonads of the specimens collected in June and the spent gonads of the September specimens suggest reproduction in summer and brooding seems unlikely but cannot be completely be ruled out.

Ophioderma hybridum is assumed to have evolved by an ancient hybridization event between the ancestors of present-day *O. longicaudum* and *O. zibrowii*, which is thought to explain the high morphological variability observed in *O. hybridum* (Stöhr et al., 2020). Indeed, genetic divergence among the species of this complex is very recent. Separation of *O. longicaudum* from *O. zibrowii* was estimated, very roughly, at ~220,000 generations ago by Weber et al. (2019) and the hybridization event that gave rise to genetic cluster C4 (*O. hybridum*) is dated to around 90,000 generations ago. Translating generation numbers to time is not straightforward for long lived species but we can use an independent information: Lessios & Hendler's (2022) dated phylogeny allows estimating that *O. longicaudum* and the *O. hybridum* from Tunisia (there, the mitochondrial lineages are well separated and correspond with morphologies) separated more than 2.5 million years ago, based on the single marker COI.

In Weber et al. (2019), successful identification of six isolated genetic clusters was possible but, this was based on multilocus genotypes at 31 genetic markers. Such a genotyping work was far beyond the scope of the present study. The two markers sequenced in this study were chosen because they were the only ones allowing to diagnose or exclude a species other than *O. guineense,* but we cannot rule out other hypotheses to explain the great morphological disparity of *Ophioderma* from the Bay of Biscay. Previous (but scanty) data suggest that hybridization may occur between *O. africanum* and *O. longicaudum*

because, although both haplogroups are relatively divergent (~14 substitutions), some *O. longicaudum* individuals (diagnosed as such based on multilocus genotypes) harboured haplotypes (COI marker) typical of *O. africanum* (Weber et al., 2019, Fig S1). This may be caused by hybridization events that occurred in places where these species are sympatric. Similarly, although this is not the most parsimonious hypothesis, we cannot exclude that *O. hybridum* and *O. longicaudum* hybridize or hybridized in the Bay of Biscay leading them to share COI haplotypes. This could explain observations of *O. hybridum* morphologies with *O. longicaudum* COI haplotypes. In Algeria, nearly all specimens displayed morphological characteristics overlapping between two or more species from the complex *O. longicaudum,* most often between *O. longicaudum, O. zibrowii* and *O. hybridum* (Lebouazda et al., 2022), suggesting that the species delimitated in Stöhr et al 2020 may hybridize or that their range of characteristics may have been underestimated due to limited geographical coverage for individual species.

Bathymetric and ecological differences have been found to separate species, e.g., in the genus *Acrocnida* Gislén, 1926 (Muths et al., 2006; Stöhr & Muths, 2010). In Tunisia, *O. hybridum* was found at very shallow depths (0.3-3 m) in two places which are located between two sites where *O. longicaudum* was found at 10-20 m depth, supporting that both species have different depth preferences (Weber, 2015) but only 23 specimens with bathymetric data from two localities have been collected for *O. hybridum* (Stöhr et al., 2020). In Crete, *O. longicaudum* and *O. zibrowii* were found in the same dives but displayed very significant differences in their depth distributions, the latter being more dominant between 1-3 m and the former being dominant between 3-12 m ($p < 0.001$) (Weber et al., 2014) (Table 1). The specimens used for genetic analyses here were collected at 5-8 m depth, which corresponds with the preferred depth range of *O. longicaudum* (Weber et al., 2014), but specimens in the previous studies were collected as deep as 40 m. The specimens from the Swedish Museum of Natural History invertebrate collection include specimens ranging from depths 0 to 30 m (182 lots = 532 specimens). Previous records of *Ophioderma* from the French Basque coast were collected at intertidal depths (de Casamajor et al., 2017; Huguenin et al., 2018). These specimens likely correspond to *O. longicaudum.* However, genetic analyses would be necessary to confirm this hypothesis. Additional specimens should be collected from a broader area to establish the distribution range of *O. longicaudum* more accurately.

The observed variation in morphology and colour pattern may be inherent to the *O. longicaudum* genome. Knowledge of the ecological requirements of these species of *Ophioderma* is extremely limited, but they can be expected to compete and adapt to different niches, e.g., the brooding *O. zibrowii* is assumed to have adapted to the nutrient poor conditions in the Eastern Mediterranean Sea by providing for its young (Boissin et al., 2011; Stöhr et al. 2009). Molecular studies are helpful to better understand the species limits, evolutionary processes, and population connectivity.

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References

Bannar-Martin K.H., Kremer C.T., Ernest S.K.M., Leibold M.A., Auge H., Chase J., Declerck S.A.J., Eisenhauer N., Harpole S., Hillebrand H., Isbell F., Koffel T., Larsen S., Narwani A., Petermann J.S., Roscher C., Cabral J.S. & Supp S.R. 2018. Integrating community assembly and biodiversity to better understand ecosystem function: The Community Assembly and the Functioning of Ecosystems (CAFE) approach. *Ecology Letters*, 21: 167-180. Doi: 10.1111/ele.12895

Boissin E., Stöhr S. & Chenuil A. 2011. Did vicariance and adaptation drive cryptic speciation and evolution of brooding in *Ophioderma longicauda* (Echinodermata: Ophiuroidea), a common Atlanto-Mediterranean ophiuroid? *Molecular Ecology,* 22: 4737-4755. Doi: 10.1111/j.1365-294X.2011.05309.x

Bruzelius N. 1805. *Dissertatio sistens species cognitas asteriarum, quamr. sub praesidio D.M. and J. Retzii, pro laurea modeste exhibet Nicolaus Bruzelius*. Berlingianis, Lund.

de Casamajor M.-N., Lalanne Y., Huguenin L., Marticorena J., Lissardy M., Bru N., D'Amico F. & Liquet B. 2017. BIGORNO. Biodiversité Intertidale sud Gascogne Observation et Recherche de Nouveaux Outils de surveillance et d'aide à la décision - Rapport final. R.INT.ODE/LITTORAL/LER/AR/17.001. https://archimer.ifremer.fr/doc/00371/48229/

Fenaux L. 1972. Evolution saisonnière des gonades chez l'Ophiure *Ophioderma longicauda* (Retzius), Ophiuroidea. *Internationale Revue der gesamten Hydrobiologie und Hydrographie,* 27: 257-262. Doi: 10.1002/iroh.19720570205

Greeff R. 1882. 3. Echinodermen beobachtet auf einer Reise nach der Guinea-Insel Sao-Thomé. *Zoologischer Anzeiger,* 105: 114-120, 135-139, 156-159.

Hendler G. 1991. Ophiuroidea. In: *Reproduction of Marine Invertebrates* (Giese A.C., Pearse J.S. & Pearse V.B. eds), pp. 355-511. Pacific Grove: Boxwood Press: New York & London.

Huguenin L., Lalanne Y., Bru N., Lissardy M., d'Amico F., Monperrus M. & de Casamajor M.-N. 2018. Identifying benthic macrofaunal assemblages and indicator taxa of intertidal boulder fields in the south of the Bay of Biscay (northern Basque coast). A framework for future monitoring. *Regional Studies In Marine Science,* 20: 13-22. Doi: 10.1016/j.rsma.2018.03.012

Kamcha R.E., Boutoumit S., Bououarour O., Pouzet P., Maanan M., Maanan M., Benhoussa A. & Bazairi H. 2023. New insights into the benthic macrofauna composition and structure in a southern-west Mediterranean coastal lagoon after restoration actions: Spatial and Seasonal patterns. *Regional Studies in Marine Science*, 60: 102820. Doi: 10.1016/j.rsma.2023.102820

Lebouazda Z., Mezali K., Khodja I. & Soualili D.L. 2022. Morphological distinction of the *Ophioderma* Müller & Troschel, 1840 species (Echinodermata: Ophiuroidea: Ophiacanthida: Ophiodermatidae) from the Algerian west coast. *Zootaxa*, 5200: 301-320. Doi: 10.11646/zootaxa.5200.4.1

Lessios H.A. & Hendler G. 2022. Mitochondrial phylogeny of the brittle star genus *Ophioderma*. *Scientific Reports*, 12: 5304. Doi: 10.1038/s41598-022-08944-0

Muths D., Davoult D., Gentil F. & Jollivet D. 2006. Incomplete cryptic speciation between intertidal and subtidal morphs of *Acrocnida brachiata* (Echinodermata: Ophiuroidea) in the Northeast Atlantic. *Molecular Ecology,* 15: 3303-3318. Doi: 10.1111/j.1365-294X.2006.03000.x

Say T. 1825. On the species of the Linnaean genus *Asterias* inhabiting the coast of the U.S. *Journal of the Academy of natural sciences of Philadelphia*, 5: 141-154.

Stancyk S.E. 1974. *Life history patterns of three estuarine brittlestars (Ophiuroidea) at Cedar Key, Florida*. PhD Thesis, University of Florida, Floride. XX°pp.

Stöhr S., Boissin E. & Chenuil A. 2009. Potential cryptic speciation in Mediterranean populations of *Ophioderma* (Echinodermata: Ophiuroidea). *Zootaxa,* 2071: 1-20. Doi: 10.11646/zootaxa.2071.1.1

Stöhr S. & Muths D. 2010. Morphological diagnosis of the two genetic lineages of *Acrocnida brachiata* (Echinodermata: Ophiuroidea) with description of a new species. *Journal of the Marine Biology Association of the United Kinddown,* 90: 831-843. Doi: 10.1017/S0025315409990749

Stöhr S., Weber A.A.-T., Boissin E. & Chenuil A. 2020. Resolving the *Ophioderma longicauda* (Echinodermata: Ophiuroidea) cryptic species complex: five sisters, three of them new. *European Journal of Taxonomy,* 600: 1-37. Doi: 10.5852/ejt.2020.600

Weber A.A.-T., Stöhr S. & Chenuil A. 2014. Genetic data, reproduction season and reproductive strategy data support the existence of biological species in *Ophioderma longicauda*. *Comptes Rendus Biologies,* 337: 553-560. Doi: 10.1016/j.crvi.2014.07.007

Weber A.A.-T. 2015. Etude écologique et génétique du complexe d'espèces cryptiques *Ophioderma longicauda* (Ophiuroidea: Echinodermata): comparaison entre lignées incubantes et lignées produisant des larves planctoniques. PhD Thesis, Aix-Marseille University. 224 pp.

Weber A.A.-T., Mérigot B., Valière S. & Chenuil A. 2015. Influence of the larval phase on connectivity: strong differences in the genetic structure of brooders and broadcasters in the *Ophioderma longicauda* species complex. *Molecular Ecology,* 24: 6080-6094. Doi: 10.1111/mec.13456

Weber A.A.-T., Stöhr S. & Chenuil A. 2019. Species delimitation in the presence of strong incomplete lineage sorting and hybridization: lessons from *Ophioderma* (Ophiuroidea: Echinodermata). *Molecular Phylogenetics and Evolution,* 131: 138-148. Doi: 10.1016/j.ympev.2018.11.014