

Article

The Enigmatic Hadal Ophiuroid Has Found Its Place: A New Family Abyssuridae Links Ultra-Abyssal and Shallow-Water Fauna

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Abstract

Severely understudied and poorly known ultra-abyssal (hadal) brittle-stars of the genus *Abyssura* were collected during a recent expedition to the Japan Trench at depths between 6183 and 6539 m and were examined for the first time for both their molecular and detailed morphological data. To date, family-level assignment of the genus *Abyssura* remains a complete enigma, despite a recent major reorganization of ophiuroid classification. In this study, we infer an all-family level phylogeny of the class Ophiuroidea and find phylogenetic placement for *Abyssura*, which turns out to be a sister taxon of another little-known ophiuroid genus, *Ophiambix*, found in hot-vent and cold-seep environments in association with sunken wood at depths between 146 and 5315 m. The sister relationship between the hadal genus *Abyssura* and the shallow-water-to-abyssal genus *Ophiambix* is robustly supported by our molecular data, and both external and micromorphological data for these genera are highly consistent. No similar taxa have been found in any of the currently recognized 34 ophiuroid families. Therefore, the genera *Abyssura* and *Ophiambix* are assigned to the new family, Abyssuridae fam. nov. This new family shows features of paedomorphic reduction and elucidates the linkage between fauna from both the shallower and the deepest parts of the world's oceans and provides new insights into the global bathymetric, biogeographic, and diversity patterns of organisms.

Keywords: molecular analysis; morphological data; new family; ophiuroids

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1. Introduction

The phylogenetic, taxonomic, and evolutionary understanding of the echinoderm class Ophiuroidea (brittle-stars) has undergone dramatic revision over the past decade [1,2]. Recent data on ophiuroids have demonstrated their key importance for clarifying global deep-sea distributional and biogeographic patterns [3]. However, a “dark diversity of ophiuroids” has recently been revealed [4], and many taxa still have unassigned status at the family level [5]. The hadal (ultra-abyssal) zone is the deepest marine environment, at a depth of over 6000 m [6,7]. There are exceedingly few ophiuroid species recorded from depths below 6000 m. Until recently, only about 14 hadal species and subspecies with confirmed status are known [1,7–10].

From the hadal zone of the North-West Pacific deep-sea trenches, including those located near Japan, an ophiuroid coined as the genus *Abyssura* (reflecting its ultra-abyssal

range) has been described and further recorded [8,11]. Despite its relative abundance, although restricted to only a few deep-sea trenches [8], until recently, no definite phylogenetic and taxonomic assessment for *Abyssura* has ever been made, and the assignment of this taxon to a family remained a complete enigma [5]. Intriguingly, *Ophiambix* [1], morphologically similar to the *Abyssura* genus, has been placed throughout history in four different families and, in a similar way to *Abyssura*, has remained an unassigned, truly enigmatic taxon [2,5]. Compared to *Abyssura*, *Ophiambix* is known from the relatively shallow depth of a few hundred meters to deep abyssal basins connected with hot-vent or cold-seep environments and is commonly associated with sunken wood [12,13]. Thus, we have a very interesting case that deserves not only particular, but also general attention: there are two morphologically similar (to a considerable extent) ophiuroid genera, *Ophiambix*, which is bathymetrically distributed at least starting from very shallow depths (about 100–200 m), and ultra-abyssal *Abyssura*, which inhabits up to more than 6000 m depth, and this makes a true “shallower–deeper” contrast, but systematic and phylogenetic placement of these two genera have, coincidentally, also been highly controversial throughout the history of ophiuroid studies, and currently their position remains completely unsettled. To date, molecular phylogenetic data have been obtained only for eight ultra-abyssal species of brittle-stars with a definite identification (Table 1), and for the genus *Abyssura*, the molecular data were never presented previously.

Table 1. The confirmed records of the hadal ophiuroids inhabit depth below 6000 m, their past and present family placements, and the availability of the molecular phylogenetic data. Nine records with uncertain identification listed in [10] are not included.

Species (Alphabetic Order)	Previous Family Placement	Current Family Placement	Depth Range, Meters	Distribution	Molecular Data	Reference
<i>Abyssura brevibrachia</i> Belyaev & Litvinova, 1976	Ophiuridae, Ophiolepididae s.str., “Ophiurida incertae sedis”	Abyssuridae fam. nov.	6156–7295	Japan, Kuril- Kamchatic, Aleut Trenches	Present study	[1,8,14]; present study
<i>Amphiophiura bullata</i> (Thomson, 1877)	Ophiuridae, Ophiolepididae s.l.	Ophiopyrgidae	2268–6035	Atlantic, Indian Oceans, Antarctic waters	[4]	[10,15,16] Taxonomy of “ <i>A. bullata</i> ” complex is unresolved
<i>Amphiophiura bullata vitjazi</i> Litvinova, 1971	Ophiuridae, Ophiolepididae s.l.	Ophiopyrgidae	6810	Ryukyu Trench	Absent	[15], it was recorded from North Atlantic (5100 m) [9] without confirmation; assignment of data for this taxon in [4] is uncertain
<i>Amphiophiura convexa</i> (Lyman, 1878)	Ophiuridae, Ophiolepididae s.l.	Ophiopyrgidae	1950–6810	North Pacific	[4]	[10,15,16]
<i>Bathylepta pacifica</i> Belyaev & Litvinova, 1972	Ophiroleucidae	“Ophiurida incertae sedis”	5740–8006	Bougainville, New Hebrides Trenches	Absent	[1,5,10,17]

Table 1. Cont.

Species (Alphabetic Order)	Previous Family Placement	Current Family Placement	Depth Range, Meters	Distribution	Molecular Data	Reference
<i>Ophiacantha cosmica</i> Lyman, 1878, s.l.	Ophiacanthidae	Ophiacanthidae	3566–6235	Pacific Ocean, Antarctic waters	[4]	[16,17]; present study
<i>Ophiocymbium rarispinum</i> Martynov, 2010	Ophiacanthidae, Ophiomyxidae s.l.	“Ophioscolecidae” s.l.	6740–6850	Izu-Bonin Trench	Absent	[1] <i>O. cf. rarispinum</i> was reported in [18] from Clarion- Clipperton Zone (5206 m)
<i>Ophiocymbium tanyae</i> Martynov, 2010	Ophiacanthidae, Ophiomyxidae s.l.	“Ophioscolecidae” s.l.	5204–6850	Izu-Bonin Trench, Clarion- Clipperton Zone	[18,19]	[1,18,19]; present study
<i>Ophioplinthus madseni</i> (Belyaev & Litvinova, 1972)	Ophiuridae, Ophiopodidae s.l.	Ophiopyrgidae	6675–7230	Kuril- Kamchatic, Japan Trenches	Absent	[10,17]
<i>Ophiotrypa simplex</i> Koehler, 1897	Ophiuridae	Ophiopodidae	3595–6487	Atlantic, Indian, Pacific Oceans, Javanese Trench	[4]	[4,9,10]; present study
<i>Ophiura bathybia</i> H.L. Clark, 1911	Ophiuridae, Ophiopodidae s.l.	Ophiuridae	2870–6328	North Pacific, including Aleutic and Kuril- Kamchatic Trenches	Absent	[10]
<i>Ophiuroglypha fendouzhe</i> Nethupul, Stöhr, Zhang, 2023	Ophiopyrgidae	Ophiopyrgidae	7729	Philippine sea, central rift zone	[20]	[20]
<i>Ophiuroglypha irrorata</i> (Lyman, 1878) s.l.	Ophiuridae, Ophiopodidae s.l.	Ophiopyrgidae	2510–7340 (lowest depth ranges for <i>O. irrorata</i> s.l. are given as 91 m [10] or 403 m [9], which definitely belong to a different species)	Atlantic, Indian, and Pacific Oceans	[4]	[10]
<i>Perlophiura profundissima</i> Belyaev & Litvinova, 1972	Ophiuridae	Ophiosphalmidae	2265–8135	Atlantic, Indian and Pacific Oceans	[4]	[4,9,10,17]; present study

To fulfill this significant gap in knowledge, in this study, molecular and morphological data from recently collected *Abyssura* specimens from hadal depths below 6000 m have been obtained for the first time and combined with molecular data for the genus *Ophiambix* from both relatively shallow bathyal (200–500 m) and deeper bathyal depth over 1000 m (the latter data also obtained for the first time) in an all-family phylogeny of the class

Ophiuroidea. Notably, two enigmatic taxa with similar morphology [1,14] (present study) have been recovered as related sister taxa. This allows for the robust establishment of a new family for *Abyssura* and *Ophiambix* by applying both very consistent molecular and morphological data, which therefore links both relatively shallow and ultra-abyssal environments and provides clues for the evolutionary origin of the hadal genus *Abyssura*.

This remarkable discovery goes far beyond solving a purely taxonomic problem because it allows for the placement of one of the few deepest extant ophiuroid *Abyssura* on the phylogenetic tree, making respective taxonomic placement and, hence, further reducing the amount of unknown “dark ophiuroid diversity” [4] possible, which contributes to our understating of global biogeographic and organism diversity patterns.

2. Materials and Methods

2.1. Sampling

Twenty specimens of *Abyssura brevibrachia* Belyaev & Litvinova, 1976 were collected by 4 m Oregon-type beam trawl during a recent KH-23-5 cruise of R.V. Hakuho-maru of the Japan Agency for Marine-Earth Science and Technology (JAMSTEC) off northern Japan, at stations F9 (39°32.540' N 144°9.524' E–39°31.961' N 144°9.705' E, 26 September 2023, depth 6522–6539 m) and C5 (41°28.411' N 146°6.803' E–41°28.519' N 146°7.632' E, 21 September 2023, depth 6183–6186 m). The specimens were preserved in 99% ethanol and deposited in the National Museum of Nature and Science (NSMT E-14743 and 14744). One paratype of *Ophiambix kagutsuchi* Okanishi, Kato, Watanabe, Chen & Fujita, 2020 (NSMT E-13069) and two *Ophiocamax polyploca* H.L. Clark, 1911 specimens (NSMT E-14591 and 14722) that were previously deposited in NSMT were also examined. For comparative purposes, specimens from the Zoological Museum of Lomonosov Moscow State University (ZMMU) were been investigated.

2.2. Nomenclatural Acts

According to the International Commission on Zoological Nomenclature (ICZN), this article, in electronic Portable Document Format (PDF), represents a published work; thereby, all new nomenclatural acts are effectively published under that ICZN rules for the electronic edition alone. All new nomenclatural acts have been registered in the online registration system for the ICZN in ZooBank. The ZooBank Life Science Identifier (LSID) for this publication is [urn:lsid:zoobank.org: pub:19EAF6DF-6129-4BAA-81F8-2389632E39BD]. All LSIDs can be resolved and the associated information viewed (by appending the LSID to the prefix <http://zoobank.org/>) using any standard web browser.

2.3. Morphological Analysis

External and internal morphological peculiarities were studied using a stereomicroscope and digital cameras (Nikon D-810, Nikon Corporation, Tokyo, Japan). The ophiuroid ossicles were extracted and processed in 5% sodium hypochlorite solution. The ossicles were rinsed in water and 70% ethanol, then dried, mounted on stubs using carbon tape, coated with gold and palladium, and, finally, examined using scanning electron microscopes (CamScan Series II (Cambridge Instruments, Cambridge, UK), JSM 6380, JSM IT 200 (Jeol Ltd., Tokyo, Japan), QuattroS (Thermo Fisher Scientific, Waltham, MA, USA). The terminology for ophiuroid morphology has been used following a well-recognized and widely accepted review of morphology of ophiuroid skeletal elements [1], and in diagnoses of the currently accepted ophiuroid families [5].

2.4. Molecular Analysis

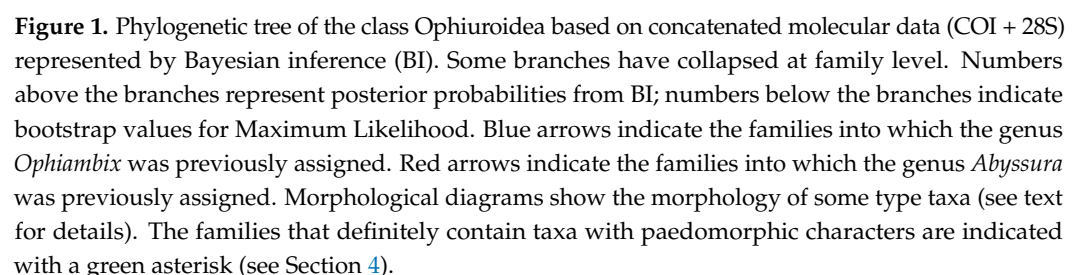
Sequences of the mitochondrial cytochrome oxidase subunit I gene (COI), and the nuclear 28S rDNA (C1-C2 domain) were obtained for one *Abyssura brevibrachia*, one *Ophiambix kagutsuchi*, and two *Ophiocamax polyploca*. Small pieces of tissue were used for DNA extraction with a DNeasy Blood & Tissue Kit (QIAGEN) following the protocol provided by the manufacturer. The amplification of the COI gene was performed with modified for this study primers, based on the primers developed by O'Hara et al., 2014 [21]: Oph-CO1-F-mod TTTCHACTAATCAYAAGGAYATWGG and Oph-CO1-R CTTCAAGGRTGWCCRAARAAYCA. The 28S rDNA primers that were used for amplification are as follows: 28S-C1 ACCCGCTGAATTTAAGCAT [22], and 28S-C2 TGAAGTCTCTCTTCAAAGTTCTTTTC [23]. The amplifications were performed with an initial denaturation for 10 min at 95 °C, followed by 40 cycles of 30 s at 95 °C, 60 s at 45 °C, and 60 s at 72 °C, with a final extension of 7 min at 72 °C (the COI amplification) and with an initial denaturation for 3 min at 94 °C, followed by 40 cycles of 20 s at 94 °C, 40 s at 50 °C, and 40 s at 72 °C, with for 7 min at 72 °C a final extension (the 28S amplification). Sequencing reactions were analyzed using an Applied Biosystems 3730 DNA Analyzer (Thermo Fisher Scientific, Waltham, MA, USA), for both strands proceeded with the ABI PRISM® BigDye™ Terminator v. 3.1 (the same manufacturer). COI sequences were translated into amino acids for additional verification and confirmation of the alignment. The sequences were deposited in GenBank (Tables S1 and S2, all new numbers highlighted in bold).

Eight new sequences combined with 242 publicly available sequences were examined (Table S1). In total, 131 specimens, including 8 outgroup specimens from the classes Asteroidea, Echinoidea, and Crinoidea, were analyzed. The species dataset was selected in such a way as to cover all 34 currently existing families [2,4,5] of class Ophiuroidea. Separate analyses were conducted for COI (1385 bp), 28S (1049 bp), and concatenated sequences of the two markers (2434 bp). Additionally the separate analyses were performed for clarification of the molecular–phylogenetic relationships among the Ophioscolecida taxa (in total 76 sequences, Table S2). Separate analyses were conducted for COI (657 bp), 28S (999 bp), and two concatenated markers (1656 bp). The MAFFT algorithm [24] was used to align the sequences. The evolutionary models were selected using MEGA11 [25]. The GTR + G + I model was chosen for the concatenated dataset of class Ophiuroidea and the GTR + G model was chosen for the concatenated dataset of order Ophioscolecida. Both Bayesian inference (BI) and Maximum Likelihood (ML) were used to infer the evolutionary relationships. Bayesian analyses were performed in MrBayes 3.2 [26] for 107 generations and four chains. Markov chains were sampled every 500 generations. Maximum Likelihood (ML) analyses were performed in RAxML 7.2.8 [27] with bootstrap in 1000 pseudo-replications. The final phylogenetic tree representations were rendered in FigTree 1.4.2 (<http://tree.bio.ed.ac.uk>, accessed on 3 February 2023). Uncorrected p-distances were calculated in MEGA11 [25].

3. Results

3.1. Molecular Phylogeny

For the class Ophiuroidea dataset, the Bayesian Inference (BI) and Maximum Likelihood (ML) analyses based on the concatenated COI+28S dataset yielded trees with identical topologies at the family level (Figure 1). It is very important that the selected dataset encompasses all of the currently known ophiuroid families (34 currently existing families) and the topology of the obtained tree corresponds well with all of the major features of a recent phylogeny, illustrating the relationships and phylogenetic diversity of the abyssal eastern Pacific Ocean fauna reconstructed using a super-matrix approach, including data



Furthermore, and also crucially, almost all of the family clades represented in the present study have high support (Figure 1). Specimens from the families Ophiotrichidae, Ophiactidae, Ophiernidae, Ophiopsilidae, Ophiocomidae, Ophiacanthidae, Clarkcomidae, Ophiocamacidae, Ophioleucidae, Astrophiuridae, Ophiosphalmidae, Ophiomusaidae, and Asteronychidae formed a maximum-supported clade (PP = 1, BS = 100). Specimens from other families were found to have a well-supported lineage: Ophiopholidae (PP = 1, BS = 95); Hemieuryalidae (PP = 0.81, BS = 75); Ophiolepididae (PP = 1, BS = 97); Ophionereididae (PP = 1, BS = 99); Ophiodermatidae (PP = 1, BS = 81); Ophiomyxidae (PP = 1, BS = 84); Ophiotomidae (PP = 1, BS = 99); Ophiopteridae (PP = 1, BS = 96); Ophiopezidae (PP = 1, BS = 99); Ophiopyrgidae (PP = 1, BS = 97); Ophiuridae (PP = 1, BS = 97); Gorgonocephalidae (PP = 1, BS = 92); and Euryalidae (PP = 0.85, BS = 91). Two *Ophiocamax polyploca* specimens clustered together, with all *Ophiocamax* species in a clade of Ophiocamacidae (PP = 1, BS = 100). The genetic distance values between *Ophiocamax polyploca* and the *Ophiocamax vitrea* are 6.53% for COI (658 bp), which indicates that *Ophiocamax polyploca* H.L.Clark, 1911 and *Ophiocamax vitrea* Lyman, 1878 [28] are different species. The validity of *Ophiocamax polyploca* H.L.Clark, 1911 (original description in [29]: 193–195, Figure 90) is therefore reinstated here. Compared to the type specimen of *O. vitrea* (BMNH 1882.12.23.65, Banda Sea, Kai Islands, 236 m, 12 mm disk diameter), the potential diagnostic character of *O. polyploca* includes at least a more pronounced narrow-elongate distal part of the oral shield, present in the studied type specimens of *O. polyploca* (including syntype USNM 25588, mentioned as “type” in original description [29] from Sato-misaki, Kagoshima Pref., Japan, 278 m, 17 mm disk diameter; syntype USNM 26178, Kagoshima Bay, 155 m, 7 mm disk diameter; syntype USNM 26039, Fukue Island, Nagasaki Pref., Japan, 254 m, 8 mm disk diameter) and specimens of *O. polyploca*, which were used in the present study for molecular analysis (NSMT E-14591, exactly from the type locality of *O. polyploca* in Sato-misaki, 109–145 m, 5 mm disk diameter; NSMT E-14722, close to the type locality in Kagoshima Pref., ca 100–150 m, 8 mm disk diameter). More complex morphological similarities and differences can be further revealed between *O. polyploca* and putatively “polymorphic” “*O. vitrea*”, with potential additional hidden diversity. Amphiuroidae and Amphilepididae form the paraphyletic group (PP = 0.62, BS = 99), as also found in [4].

The second huge paraphyletic group in [4] is Ophioscolecidae + Ophiohelidae. In our phylogenetic tree, the species belonging to the families Ophioscolecidae and Ophiohelidae formed four separate clades. *Ophiiotholia*, *Ophiomyces*, *Ophiophrura*, and *Ophiocymbium* species clustered together in a separate clade with high support (PP = 1, BS = 98). *Ophioscolex*, *Ophioleptoplax*, and *Ophiologimus* species clustered together in another separate clade with high support (PP = 1, BS = 90). *Abyssura brevibrachia* was placed in a sister clade with the well-supported (PP = 0.99, BS = 91) clade of the morphologically similar genus *Ophiambix* (Figure 1). This clade is a sister taxon, but with low support (PP = 0.87, BS = 29) to the specimens attributed to *Ophiuroconis pulverulenta* (Lyman, 1879). The joint clade including *Abyssura* and *Ophiambix* is well-supported (PP = 0.92, BS = 89) and is referred to here as Abyssuridae fam. nov.

For the order Ophioscolecida dataset, the Bayesian Inference (BI) and Maximum Likelihood (ML) analyses based on the concatenated COI+28S dataset yielded similar results (Figure 2). All Ophioscolecida taxa constituted a maximum-supported clade (PP = 1, BS = 100). *Abyssura brevibrachia* was placed in a sister clade with the well-supported (PP = 1, BS = 89) clade of the morphologically similar genus *Ophiambix* (Figure 2) that is also similar the results of the molecular-phylogenetic analyses of the full Ophiuroidea dataset (Figure 1). *Abyssura brevibrachia* and four *Ophiambix* specimens formed a separate

well-supported (PP = 1, BS = 98) single clade, separate from all Ophioscolecida taxa, that confirms the Abyssuridae fam. nov. *Ophiomyces*, *Ophiolithia*, and *Ophiiohelidae* sp. clustered together in a clade Ophiiohelidae. Ophioscolecidae demonstrated polyphyly and can potentially be divided into three separate families (Figure 2, marked in gray). More accurate attribution of the taxa available in GenBank and larger molecular dataset are necessary in order to be able to take a decision on the question.

Nevertheless, all of the conducted molecular analyses reveal a well-supported clade corresponding to the Abyssuridae fam. nov. (Figures 1 and 2).

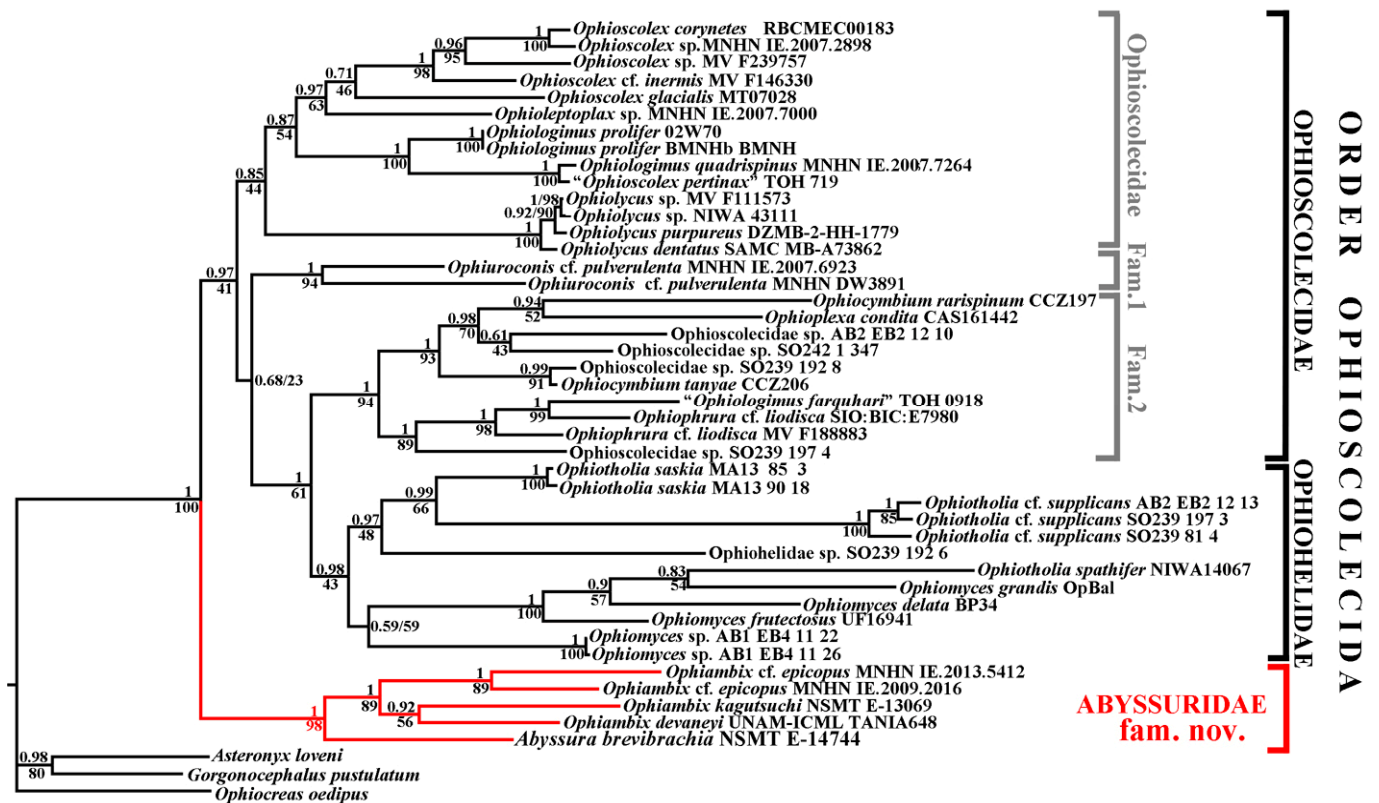


Figure 2. Phylogenetic tree of the order Ophioscolecida based on concatenated molecular data (COI + 28S) represented by Bayesian inference (BI). Numbers above the branches represent posterior probabilities from BI; numbers below the branches indicate bootstrap values for Maximum Likelihood. Abyssuridae fam. nov. clade is marked in red. The potential division within Ophioscolecidae is marked in gray. The current taxonomy of the order Ophioscolecida and the families Ophioscolecidae and Ophiiohelidae is indicated in black.

3.2. Systematic Taxonomy

Class: Ophiuroidea.

Order: Ophioscolecida.

Abyssuridae fam. nov.

urn:lsid:zoobank.org:act: 921B112F-27AB-4E35-A083-DF796C3E906F.

Diagnosis: Disk fully scaled, without evident skin (commonly termed “naked” in ophiuroids) or covered with small granules and spinelets, radial shields present. Genital papillae and arm combs absent. Dental plate entire, sockets small reduced holes, not perforating. Jaws (oral plates) covered with a few weak papillae, no clusters. Small spiky teeth. Arms flattened, both dorsal and ventral arm plates present. Arm spine articulation distinctly subparallel, with nearly equal muscle and nerve openings, distinct horseshoe-shaped ridges and surrounding lower ridges are absent. Parasol-shaped spines absent.

Tentacle pores large. Tentacle scales absent or reduced. Vertebrae streptospondylous, not keeled.

Genera included: *Abyssura* Belyaev & Litvinova, 1976, *Ophiambix* Lyman, 1880.

Remarks: The genera *Abyssura* and *Ophiambix* demonstrate complex, multilevel similarities according to morphological and molecular data. Particularly, *Abyssura* and *Ophiambix* uniquely share a similar arm spine articulation: the widely recognized character in taxonomy at all levels of the class Ophiuroidea [1,5,14]. The distinctly subparallel arm spine articulations well distinguish *Abyssura* and *Ophiambix* from any other taxa of the order Ophioscolecida (Table 2, Figure 1). Furthermore, the shape of the vertebrae is essentially similar in *Abyssura* and *Ophiambix*, including a considerably reduced streptospondylous articulation. General external patterns of the flattened arms, weakly developed oral papillae and teeth, and large tentacle pores with reduced or absent tentacle scales are also similar in *Abyssura* and *Ophiambix*. All of this morphological evidence, together with the robust, highly supported placement of the genera *Abyssura* and *Ophiambix* as closely related sister groups according to the molecular phylogenetic analyses (Figures 1 and 2), leave no doubt that both these genera together form the new family Abyssuridae (Table 2). These consolidated evidence exclude any potential considerations of “convergent similarities” with taxa from any other orders of the class Ophiuroidea [1,5] (Figure 1).

Both *Abyssura* and some species of *Ophiambix* (such as *O. meteoris* Bartsch, 1983 and *O. kagutsuchi* Okanishi et al., 2020) also share, in part, similar shapes of arm spines (Figure 3), although in other species of *Ophiambix*, the spines are more differentiated (*O. aculeatus* Lyman, 1880, *O. devaneyi* Paterson, 1985, *O. epicopus* Pateson & Baker, 1988, and *O. macrodonta* Okanishi et al., 2020) [12,13]. Together with some differences in teeth morphology, this may imply a necessity of a further genus-level differentiation within the current genus *Ophiambix*. The main differences between the genera *Abyssura* and *Ophiambix* include the complete absence of the disk granules/spinelets and tentacle scales in *Abyssura* and the generally more distinct appearance of the arms and disk compared to *Ophiambix*. The latter genus instead commonly possesses small granules/spinelets on the disk and shows the presence of tentacle scales (although in various degrees of reduction [12]), as well as a smoother transition between the arms and the disk. In addition, *Abyssura* has generally more reduced oral papillae, teeth, oral shield, and arm spine articulations than those in *Ophiambix* (see also below).

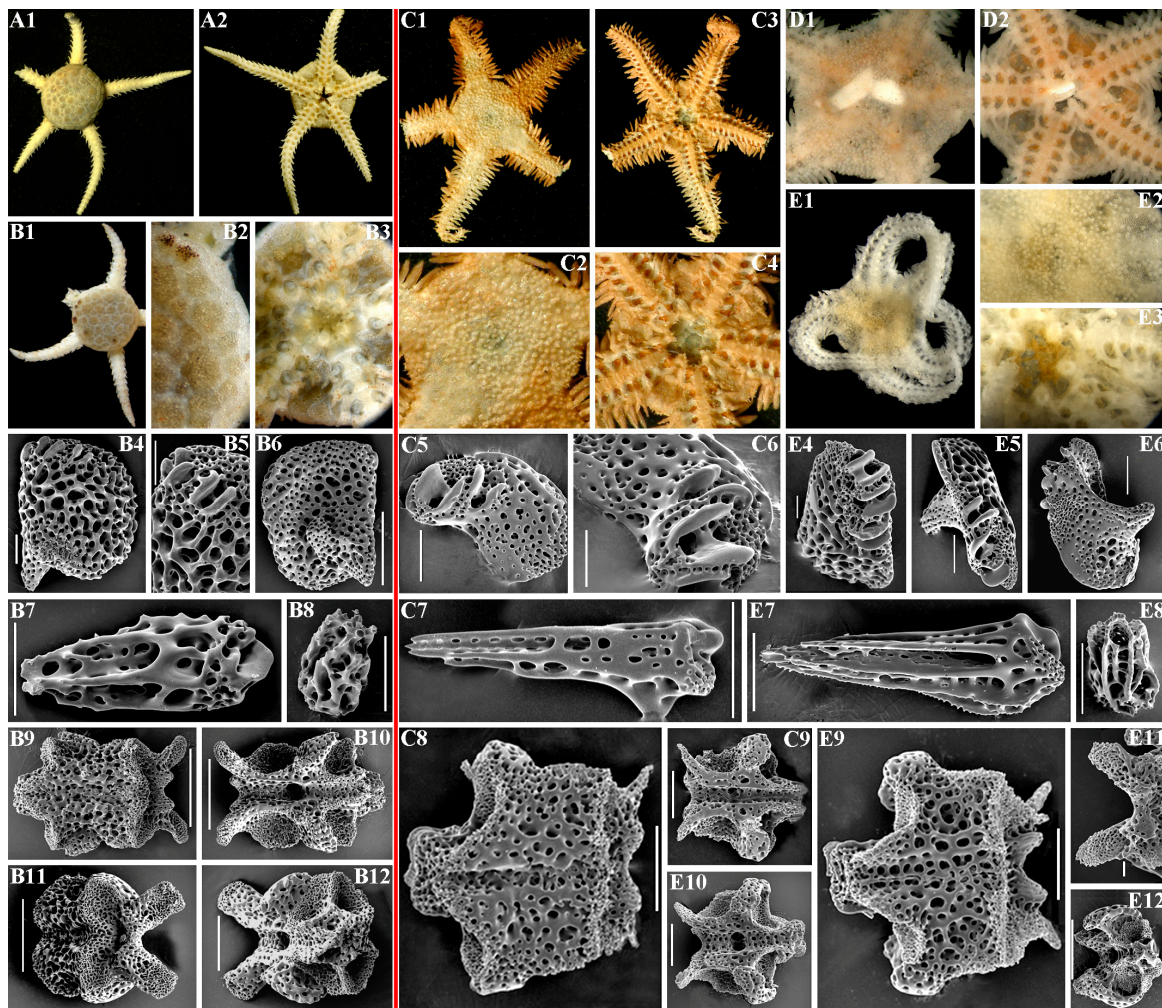


Figure 3. Morphological data for the genera *Abyssura* and *Ophiambix*. (A1,A2)—*Abyssura brevibrachia* Belyaev & Litvinova, 1976, holotype IORAS 14.304, North Pacific, Kuril-Kamchatic Trench, collected at the depth 7140 m, 5.5 mm in disk diameter. (A1)—dorsal view. (A2)—ventral view. (B1–B12)—*Abyssura brevibrachia*, NSMT E-14744, from the Japan Trench, collected at the depth 6183–6186 m, 4.8 mm in disk diameter. (B1)—dorsal view. (B2)—dorsal view, details. (B3)—ventral view, details. (B4)—lateral arm plate, dorsal side with spine articulations, SEM, scale bar 100 μ m. (B5)—lateral arm plate, spine articulations, details, SEM, 100 μ m. (B6)—lateral arm plate, ventral side, SEM, 250 μ m. (B7)—spine, SEM, 100 μ m. (B8)—spine, section, SEM, 100 μ m. (B9)—vertebra, dorsal side, SEM, 250 μ m. (B10)—vertebra, ventral side, SEM, 250 μ m. (B11)—vertebra, distal articulation, SEM, 200 μ m. (B12)—vertebra, proximal articulation, SEM, 150 μ m. (C1–C9)—*Ophiambix aculeatus* Lyman, 1880, ZMMU D-862, Indian Ocean, collected at the depth 3300 m, type species of the genus *Ophiambix*, 4 mm in disk diameter. (C1)—dorsal view. (C2)—dorsal view, details. (C3)—ventral view. (C4)—ventral view, details. (C5)—lateral arm plate, dorsal side with arm spine articulations, SEM, 150 μ m. (C6)—lateral arm plate, details of arm spine articulations, SEM, 80 μ m. (C7)—spine, SEM, 150 μ m. (C8)—vertebra, dorsal side, SEM, 120 μ m. (C9)—vertebra, ventral side, SEM, 120 μ m. (D1–D2)—*Ophiambix meteoris* Bartsch, 1983, North Atlantic, collected at the depth 5315 m, deepest known species of the genus *Ophiambix*, holotype ZSM (State Bavarian Collection), 4.1 mm in disk diameter. (D1)—dorsal view, details. (D2)—ventral view, details. (E1–E12)—*Ophiambix kagutsuchi* Okanishi, Kato, Watanabe, Chen & Fujita, 2020, paratype NSMT E-13069, Okinawa Trough, off Sakishima Island, collected at the depth 1979 m, 4 mm in disk diameter. (E1)—dorsal view. (E2)—dorsal view, details. (E3)—ventral view, details. (E4)—lateral arm plate, dorsal side with spine articulations, SEM, 50 μ m. (E5)—lateral arm plate, dorsal side with spine articulations, SEM, 100 μ m. (E6)—lateral arm plate, ventral side, SEM, 100 μ m. (E7)—spine, SEM, 100 μ m. (E8)—spine, section, SEM, 100 μ m. (E9)—vertebra, dorsal side, SEM, 100 μ m. (E10)—vertebra, ventral side, SEM, 100 μ m. (E11)—vertebra, distal articulation, SEM, 20 μ m. (E12)—vertebra, proximal articulation, SEM, 150 μ m.

Table 2. Morphological comparison of the new family Abyssuridae fam. nov., including families, to which the genera *Abyssura* and *Ophiambix* were previously assigned (Ophiuridae, Ophiopyrgidae, Ophiacanthidae, Amphiuridae, Ophiolepididae) [1,5,12,14,30] and those, to which are related according to the present molecular phylogenetic analysis (Ophioscolecidae, Ophiohelidae, Figure 1).

	Abyssuridae fam. nov.	Ophiuridae	Ophiopyrgidae	Ophiacanthidae	“Ophioscolecidae” s.l.	Ophiohelidae	Amphiuridae	Ophiolepididae
Disk	Fully scaled, naked or with granules, without evident, thick skin	Fully scaled, commonly naked, without evident, thick skin	Fully scaled, commonly naked, without evident skin, thick skin in a few currently included taxa	Fully scaled, commonly with some evident amount of skin, spines and granules, or naked (without evident skin) in some taxa	In type genus of family (<i>Ophioscolex</i>) thick skin on disk and arms, and no disk scales, in several other currently included taxa (e.g., <i>Ophiophrura</i>) some disk scales are present	Fully scaled, sac-shaped	Fully scaled, commonly naked, without evident or with thick skin	Fully scaled, commonly naked, without evident, thick skin
Arms position in relation to disk	Adjacent to disk only at basal segments	Adjacent to disk only at basal segments	Adjacent to disk only at basal segments	Adjacent to disk only at basal segments	Adjacent to disk only at basal segments	Commonly adjacent to sac-shaped disk along its whole length	Adjacent to disk only at basal segments	Adjacent to disk only at basal segments
Arm spine articulation on lateral arm plates	Subparallel ridges open at both ends, framing two openings nearly equal in size	Large irregularly rounded muscle opening on elevation and nerve opening at basis of this knob, dorsal-most articulation usually placed at an angle in relation to nerve opening. In juvenile specimens, nerve opening is reduced	Large irregularly-rounded muscle opening on elevation and nerve opening at basis of this knob, dorsal-most articulation is usually placed at angle in relation to nerve opening. In some small-sized taxa and in juvenile specimens, nerve opening is reduced	Volute-shaped articulations with large muscle opening and small slit-shaped nerve opening, and sigmoidal fold	In type genus of family, <i>Ophioscolex</i> , single-opening pattern, sometimes horseshoe-shaped with broad low border. In other currently included representatives can be double-opening articulations, somewhat in part subparallel with low dorsal lobe (e.g., <i>Ophiophrura</i> , <i>Ophiologimus</i>)	Articulation with nearly vertical dorsal and ventral lobes, connected at their proximal ends, opening into wide y- or horseshoe-shaped, bordering single muscle/nerve opening, dorsal lobe larger and bent	Nearly parallel, quite often slightly curved high ridges, elongated in proximal-distal direction, framing two openings of nearly equal	Parallel or subparallel ridges open at both ends, framing two openings nearly equal in size. The ridges are considerably depressed on the lateral plate

Table 2. Cont.

	Abyssuridae fam. nov.	Ophiuridae	Ophiopyrgidae	Ophiacanthidae	“Ophioscolecidae” s.l.	Ophiohelidae	Amphiuridae	Ophiolepididae
Umbrella (parasol)- shaped spines	Absent in all genera	Absent in all genera	Absent in all genera	Absent in all genera	Absent in all genera	Present in two from three currently included genera	Absent in all genera	Absent in all genera
Vertebrae	Not keeled, streptospondylous articulation	Keeled, zygospondylous articulation	Keeled, zygospondylous articulation	Keeled, zygospondylous, or rarely reduced towards streptospondy- lous articulation	Not keeled zygospondylous in type genus <i>Ophioscolex</i> , to partly keeled and zygospondylous (e.g., in <i>Ophiophrura</i>), or streptospondylous	Partly keeled with specific articulation	Keeled, zygospondylous articulation	Keeled, zygospondylous articulation
Tentacle pores	Large	Moderate	Moderate	Moderate	Large	Moderate	Moderate	Moderate
Tentacle scales	Reduced or absent	Commonly well-defined	Commonly well-defined	Commonly well-defined	Absent or reduced	Well-defined	Well-defined	Well-defined
Radial shield	Present	Present	Present	Present	Present	Absent	Present	Present
Oral and tooth papillae	Weakly differentiated, short	Well- differentiated, commonly spiniiform or elongate	Well- differentiated, commonly spiniiform or elongate, in small taxa may become short	Well- differentiated, commonly oval to elongate	Well-differentiated, commonly spiniiform	Well- differentiated, long, flattened, densely placed on jaws	Well-differentiated, elongate or spiniiform, tooth papillae commonly double	Well- differentiated, elongate to square
Teeth	Weakly differentiated, few in number, spiniiform	Well- differentiated, spiniiform, numerous	Well- differentiated, spiniiform, numerous, in small taxa may become fewer	Well- differentiated, commonly broadly flattened and numerous	Well-differentiated, spiniiform, numerous	Well- differentiated, spiniiform, numerous	Well-differentiated commonly broadly flattened and numerous	Well- differentiated commonly broadly flattened and numerous
Oral shield	Weakly differentiated	Well- differentiated	Well- differentiated	Well- differentiated	Weakly differentiated in genus <i>Ophioscolex</i> , in other taxa well-differentiated	Well- differentiated	Well-differentiated	Well- differentiated

4. Discussion

Until recently, the family structure of the class Ophiuroidea was relatively simple, comprising only about 16 families. Combining fine-scale micromorphological [1] and molecular data [2], most recently, the classification of the higher taxa of brittle-stars rapidly changed and expanded to over 30 extant families [5]. However, it is obvious that this is not “the last word” for high-level ophiuroid taxa, and even in the latest classification there are many morphological and molecular inconsistencies, and many genera are still not assigned even to family-level taxa [4,5].

For instance, it is very characteristic that when the new family Ophiojuridae was recently added to ophiuroid classification [31], many other problems associated with incongruence in molecular and morphological data persisted. Particularly relevant for the present case, the clade comprising the families Ophioscolecidae and Ophiohelidae is still poorly delineated and represents a morphologically highly heterogeneous assemblage without proper diagnoses [4,5] (Figure 1). Especially significant is the fact that “Ophioscolecidae” s.l. is inconsistent in the pattern of arm spine articulation (Figure 1, Table 2), which are otherwise generally conservative and represent a well-established diagnostic character at the family level [1,31]. Furthermore, when the family Ophiojuridae was proposed, the important genus *Ophiologimus* from the family Ophioscolecidae was missing from the discussion [31], despite that it, like Ophiojuridae, has many arms and that the pattern of the arm spine articulations is also similar (see relevant parts in references [1,31]). Whilst *Ophiologimus* and Ophiojuridae are distantly related according to molecular phylogenetic data [31] (present study, Figure 1), external and internal similarities may imply deeper evolutionary roots, which should be discussed during the establishment of the family Ophiojuridae. As a very relevant example related to this case, the stem genus of the family Ophioscolecidae, *Ophioscolex* (and its type species *O. glacialis* Müller & Troschel, 1842) (Table 2) evidently possesses a combination of external and microstructural characters that are partly similar to the representatives of Paleozoic group Oegophiurida [1]. At the same time, *O. glacialis* is a common Arctic ophiuroid that was originally described in the 19th century [1]. Nevertheless, exactly the family Ophiojuridae was coined as a “relict from Jurassic” [31]. In this context, *Ophioscolex glacialis* is a relict from the pre-Jurassic period, which corresponds well to at least Triassic origin of the order Ophioscolecida [2]). A similar consideration of the tight linkage between seemingly “very ancient” and “very recent” taxa can be made with respect to several other ophiuroid orders, since they also have at least Triassic origin [2]. Thus, rather than misleadingly contrasting extant taxa of the class Ophiuroidea as “relict” or “non-relict”, it would be much more productive to consider the complex, multilevel intersection of various sets of both evidently ancient and more recent characters among modern ophiuroids.

With these examples, we show that even recently separated ophiuroid families are not straightforwardly different from each other, but instead show a complicated morphological and molecular mosaic [1,2,5] (present study, Figure 1). In spite of all these complications, for example, the distinctness of the family Ophiohelidae recently has been highlighted [5,32]. Thus, if one too strictly follows the molecular data, such a well-established and morphologically distinct family as Ophiohelidae [5] (Figure 1, Table 2) may come into synonymy with the family Ophioscolecidae, to which it is obviously related (Figure 2). This, instead of furthering phylogenetic and taxonomic progress, takes us backwards and masks the contradictions that have not been overcome. Furthermore, since a majority of the ophiuroid families have very complex, partly overlapping diagnostic features, which are conjoined with a no-less-complicated phylogenetic pattern [1,2,5,31] (present study, Figure 1, Table 2), any putative lumping event will open a “Pandora’s box” where a majority of ophiuroid families, following the blurred diagnoses and complex phylogeny, could

potentially be lumped into just 2–3 very large families, thus ruining any advancement in the recent progress in ophiuroid taxonomy. Therefore, a new round of fine-scale taxonomic differentiation of the family level in the class Ophiuroidea is not just needed, but urgently necessary. Thus, the separation in the present study of the new family Abyssuridae is both a very natural and logical progression of the “recent progress” [1,2,5] in ophiuroid taxonomy. Still, there are several other ophiuroid clades that are highly inconsistent regarding morphological and molecular data that require further family-level differentiation, and this could be the subject of further studies.

Only a few confirmed genera of hadal ophiuroids have been discovered so far [7,10] (present study, Table 1). While such common abyssal-to-hadal ophiuroid species complexes as *Amphiophiura bullata* and *Ophiacantha cosmica* [9,15–17], or a recently described hadal species of the genus *Ophiuroglypha* [20], are currently firmly assigned to respective families such as Ophiacanthidae and Ophiopyrgidae [5,11], the phylogenetic and taxonomic position of the genus *Abyssura* remains a complete enigma, as this is unambiguously indicated by its current status as “Ophiurida incertae sedis” [5]. This is especially noticeable since the single known species, *Abyssura brevibrachia* Belayev & Litvinova, 1976 (Figure 3), forms bottom accumulations in the ultra-abyssal trenches of the North-West Pacific Ocean [8,11]. Therefore, the first molecular data on the genus *Abyssura* not only makes it possible to elucidate its phylogenetic position, but also contributes to our understanding of the biogeographic and ecological patterns of deep-sea biota. In addition, in this study, we present, for the first time, molecular data on *Ophiambix kagutsuchi* Okanishi et al., 2020 [13], from Japan, collected at a significant depth of 1979 m, which represents the deepest molecular data so far obtained from a representative of the genus *Ophiambix* (Figures 1–3).

It is noteworthy that the genus *Ophiambix* has been assigned to four completely different ophiuroid families during its taxonomic history—Amphiuridae, Ophiacanthidae, Ophiuridae, and Ophiolepididae [1,12,14,30]—while the genus *Abyssura*, since its first discovery, was still largely placed within the family Ophiuridae sensu lato, although morphological similarity to the genus *Ophiambix* had already been noted [14]. Thus, there is no exaggeration in the conclusion that the taxonomic placement and phylogenetic relationship of the both genera *Abyssura* and *Ophiambix* remains a complete enigma. Therefore, both the molecular and morphological data presented here clearly show that the genus *Abyssura* is related to *Ophiambix* (Figures 1–3) within the Ophioscolecida (and not within Ophiurida or Ophiacanthida, as is commonly currently assigned [5,12]) is of high importance. The morphological data for the newly collected specimens of *Abyssura brevibrachia* are essentially similar to the holotype of *A. brevibrachia* (Figure 3) restudied here.

Moreover, according to the molecular phylogenetic analysis (Figures 1 and 2), both *Abyssura* and *Ophiambix* belong precisely to the clade that includes the families Ophioscolecidae and Ophiolidae. Therefore, as a first step in further delineating this phylogenetically important basal ophiuroid complex, we established here a new family, Abyssuridae, to accommodate the genera *Abyssura* and *Ophiambix*. Both genera are morphologically consistent due to the presence of a fully scaled disk without evident skin, the presence of radial shields, arm spine articulations with subparallel ridges framing two openings nearly equal in size, non-keeled vertebrae with streptospondylous articulation, weakly differentiated oral papillae and teeth, and large tentacle pores with reduced or completely absent tentacle scales (Figure 3).

By this unique combination of characters, the new family Abyssuridae immediately differs from the family Ophiolidae, which comprises a highly peculiar taxa without a radial shield and commonly with bent arms along a sac-like disk [5,32], and from the family Ophioscolecidae, which, in contrast to Abyssuridae, possesses strongly thickened skin on the dorsal disk and arms in combination with a horseshoe-shaped single open-

ing or an elevated double-opening arm spine articulation and spiniform oral papillae (Figure 1, Table 2). Abyssuridae shares large tentacle pores and less-differentiated vertebrae with Ophioscolecidae, but these characters alone cannot be considered diagnostic at the family-level since they occur in unrelated ophiuroids [1]. The clade that now contains Ophioscolecidae, Abyssuridae, and Ophiohelidae (Figure 1) still remains partially heterogeneous (Figures 1 and 2), especially in the position of the genera *Ophiocymbium* and *Ophiuroconis*, which will require attention in further studies, including the separation of more families (Figure 2). The arm spine articulations also immediately distinguish the new family Abyssuridae from both Ophioscolecidae and Ophiohelidae because neither have such distinctly subparallel articulations. The phylogenetically closely related *Abyssura* and *Ophiambix* (Figures 1 and 2) definitely have similar external and internal characters, including generally flattened arms, weakly developed oral papillae, large tentacle pores, and uniquely share subparallel spine articulation and non-keeled vertebrae, and all of these characters in total are very consistent (Figure 3).

The family Abyssuridae fam. nov. is significantly and unambiguously differentiated from any of the four families to which the genus *Ophiambix* has been previously assigned [1,12], and, based on the high-supported placement of the family Abyssuridae within the order Ophioscolecida (Figure 2), any potential relationship to any other ophiuroid orders can be now excluded. Particularly, the families Ophiacanthidae and Ophiuridae (the latter is currently further divided into Ophiopyrgidae [2,5]) radically differs from Abyssuridae by the shape of the arm spine articulations (volute-shaped in ophiacanthids and a large irregularly round muscle opening on an elevation and a nerve opening at the basis of this knob, reduced in several taxa in ophiuroids and ophiopyrgids, Figure 1) and generally keeled vertebrae (Table 2; for definition of keeled vertebrae see, e.g., [1] p. 36). In turn, the families Amphiuridae and Ophiolepididae are partly similar to Abyssuridae in the patterns of their arm spine articulations, which is due to a common ancestral ontogenetic base [1,14], but differ significantly in their details and are immediately distinguished by very different oral frames and keeled vertebrae (Figure 1, Table 2). Furthermore, according to the present molecular phylogenetic analysis, which, importantly, in its main topology, coincides with recent multigene analyses [4], the families Ophiuridae, Ophiopyrgidae, Ophiacanthidae, Amphiuridae, and Ophiolepididae are placed in completely different clades, only distantly related to Abyssuridae (Figure 1). The present phylogeny of the selected genes is robust and encompasses all of the currently known ophiuroid families (Figure 1), and also additionally covers most of the available data for the order Ophioscolecida (Figure 2). As we highlighted, the present analyses (Figures 1 and 2) coincide with the previous phylogeny, based on transcriptomic analysis [2,4], which is the best test for the robustness of our present tree regarding the position of the new family Abyssuridae.

All other currently recognized families are very different from Abyssuridae in their combination of external and internal characters [1,5]. Regarding potential fossil calibration, since the diversification of the order Ophioscolecida occurred at least in the Jurassic [2], we expect that the origin of the family Abyssuridae can be traced from the Triassic, although respective fossils have not been uncovered so far. In this respect, it is worth repeating once again that not only is the recently established family Ophiojuridae [31] a “relict from the Jurassic”, but several family-level taxa of the order Ophioscolecida, including Abyssuridae fam. nov., could potentially be traced back to this and earlier periods.

Bathymetrically, *Abyssura* represents one of the deepest-known ophiuroids, and is one of only six confirmed species recorded at depths greater than 7000 m (Table 1). Thus, the new family Abyssuridae elegantly links the shallow-water and hadal faunas, since the six species of the genus *Ophiambix* discovered so far are known from the depth range of 146–5315 m [12,13,33]. Both shallow-water *Ophiambix* species (*O. devaneyi*, whose reported

depth range is 146–494 m [12]) and a species with a significantly deeper, bathyal lowermost occurrence (*O. kagutsuchi*, whose reported depth range is 276–1979 m [13] (this study)) are present on our tree (Figure 3). The type materials of the deepest-known species of the genus *Ophiambix*, *O. meteoris* from the abyssal depth of 5315 m, was additionally morphologically examined in this study (Figure 3(D1–D2)). Therefore, the uppermost range of the genus distribution coincides with the typical shallow-water faunal realm, while the deepest-known occurrences closely approximate the ultra-abyssal environment. Therefore, the hadal genus *Abyssura* (Figure 1), sister to *Ophiambix*, well connects the shallower and deeper ocean zones, and this represents another new result of the present study that is important for the biogeographical and evolutionary origin of deep-sea fauna [3]. In this regard, *Abyssura* and its single species is the deepest representative of the family Abyssuridae known to date (up to 7295 m, Table 1), and shows the paedomorphic appearance of a “naked” disk, without evident skin with partially masked but still evident primary plates in the center of the disk, compared to the *Ophiambix*, whose dorsal side is covered with granules (Figure 3).

Paedomorphosis is no longer considered simply an “exotic phenomenon” whose supposed rare occurrence requires special proof. Instead, the taxa with various degrees of paedomorphic characters are widespread across Metazoa, and, recently, criteria for assessment of paedomorphosis within the class Ophiuroidea were provided [34]. These criteria, along with other characters, include a fewer number of disk plates and significantly reduced oral and teeth papillae, as well as oral shield, all of which are well met in the family Abyssuridae. In this respect, paedomorphosis should not be viewed as a “fixed suite of characters”, and, in any particular taxon, different degrees of reduction in various characters may be observed. For example, such “iconic” paedomorphic genera as *Perlophiura* Belyaev & Litvinova, 1972 (order Ophiurida) or *Ophiotypa* Koehler, 1897 (order Amphilepidida) have well-defined paedomorphic characters in the form of a postlarval primary disk rosette in the adult state [5,34]. Other genera, such as *Ophiomastus* Lyman, 1878 in a turn exhibit a various degree of paedomorphic reduction in the disk plates and other characters [34]. This also applies for the new family Abyssuridae, where a significant reduction in disk plates (although not such pronounced as in *Perlophiura* and *Ophiotypa*), oral papillae and teeth definitely occurred, which is especially evident in the family stem-genus *Abyssura* (Figure 3). This is in good agreement with the fact that deep-sea organisms, including ophiuroids, more commonly exhibit paedomorphic features than shallow water taxa [34,35].

Importantly, in this study, we provide robust evidence that paedomorphic Abyssuridae is related to Ophioscolecidae and Ophiophilidae, but not to any other ophiuroid families for which previously paedomorphic taxa were particularly assessed, including Ophiopyrgidae, Ophiophthalmidae, Amphilepididae, and Ophiolipidae (Figure 1). Recent molecular phylogenetic data [4] have confirmed morphological prognoses of multiple independent formations of a similar paedomorphic organization in unrelated ophiuroid families, including the orders Ophiurida and Amphilepidida (summarized in [34]). For example, not only the disk with a fewer number of plates, but also the general shape of the subparallel arm spine articulations can be partly similar (although differing in detail [1,14]) in paedomorphic taxa of the evidently distantly related orders Ophioscolecida and Amphilepidida. This can be explained by common, partly similar early ontogenetic periods in all representatives of the class Ophiuroidea [34]. These facts have direct relevancy to the need for fine-scale taxonomic differentiation at all levels, including the family level, to highlight not only the “overall similarities” between reduced paedomorphic taxa, but also to provide details and establish particular taxa. Thus, the combination of fine-scale morphological characters and molecular phylogenetic data provides a reliable way to clearly distinguish between the putatively similar characters of paedomorphic taxa in distantly related families. The

families in which paedomorphic reductions have previously been proven are indicated by a green asterisk (Figure 1) to highlight the evidently independent origin of paedomorphic taxa within several completely unrelated families and orders of the class Ophiuroidea, including the new family Abyssuridae. The paedomorphic characters of various degree of expression may be present in other ophiuroid families, besides those indicated in Figure 1, but here we mention most of the well-established paedomorphic taxa within Ophiuroidea to clearly show that the family Abyssuridae with reduced paedomorphic features definitely originated independently.

In summary, for the first time, we provide molecular data for the previously completely enigmatic ophiuroid taxon, *Abyssura*, and robustly infer its phylogenetic position together with the genus *Ophiambix* (Figure 1), showing that both genera share unique morphological characteristics (Figure 3) that, together with the robust molecular data, allow for a new family, Abyssuridae, to be established, which is part of a necessary continuation of the recent progress [1,2,5] in the fine-scale differentiation of the family-level system of the class Ophiuroidea.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d17120827/s1>. Tables S1 and S2. Lists of specimens used for molecular analyses.

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