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Lyrodus mersinensis sp. nov. (Bivalvia: Teredinidae) another cryptic species in the *Lyrodus pedicellatus* (Quatrefages, 1849) complex

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Abstract

New data from barcode index numbers (BINs) and 28S rRNA gene sequences confirm a cryptic species pair in *Lyrodus pedicellatus* from the eastern Mediterranean and European Atlantic coasts. Therefore, it is paramount to associate the new species to a scientific name for a reliable reference system of biological information. To this end, we describe *Lyrodus mersinensis* **sp. nov.**, another cryptic species in the *L. pedicellatus* complex, and redescribe the `true´ *L. pedicellatus*. Both the description and redescription are based on molecular diagnostic characters obtained from sequences of the mitochondrial cytochrome *c* oxidase subunit I (COI) and nuclear 28S rRNA genes. The 18S rRNA gene sequences did not yield diagnostic characters to distinguish these species. A morphological diagnosis of *pedicellatus*-like *Lyrodus* species is also provided.

Key words: shipworms, teredinids, DNA barcodes, barcode index numbers (BINs)

Introduction

The majority of teredinids or shipworms, as they are commonly known, bore into wood (xylotrepy) and use it as their primary carbon source (xylotrophy) (Hoagland & Turner 1981; Distel *et al.* 2011). These highly specialised bivalves are characterised by elongate bodies and greatly reduced shells, adaptations that facilitate their wood-boring life style. In classic molluscan taxonomy, species hypotheses are based on shell morphology (Puillandre *et al.* 2012). In teredinids, however, species hypotheses cannot be based on their shell characters because of their great intraspecific variation and also interspecific similarity (Turner 1966; Voight 2015; Borges 2016). Instead, species delineation in teredinids has been based almost entirely on pallet morphology (Turner 1966; 1971; Macintosh 2012). These calcareous structures, located at the posterior end of the body flanking the siphons, are used as plugs to seal the entrance of the tunnels in the wood surface. Differenciation based only on pallet morphology has, however, failed to distinguish some species in the Teredinidae. Indeed, comparisons of life history strategies of brooding teredinids revealed cryptic species pairs in *Lyrodus* and *Teredo*. For instance, Calloway & Turner (1983) showed that populations of the morphospecies *Lyrodus pedicellatus* from Florida and California are two species with different brooding times and developmental stages at which the larvae are released into the plankton. Specimens from California were considered the `true´ *L. pedicellatus* (Quatrefages, 1849), whereas the population from Florida was reinstated as *L. floridanus* (Bartsch, 1922).

More recently, a phylogenetic analysis using mitochondrial cytochrome *c* oxidase subunit I (COI) and nuclear 18S rRNA gene sequences showed that northeast Atlantic and eastern Mediterranean populations of the morphospecies *Lyrodus pedicellatus* are putative cryptic species according to the unified species concept (USC), which defines species as separately evolving metapopulation lineages (De Queiroz 2007). Both COI and 18S maximum-likelihood (ML) phylograms sorted out the Atlantic and Mediterranean lineages with robust bootstrap support (99% in COI and ≥ 80% in 18S) (Borges *et al.* 2012). Reciprocal monophyly was used as a primary

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criterion to recognise the northeast Atlantic and eastern Mediterranean populations of *L. pedicellatus* as independent species. This is because only after sufficient haplotype extinction will species be recovered as monophyletic with respect to each other (Kizirian & Donnelly 2004). Genetic divergence in COI (Kimura 2 parameter, hereafter K2P) further supported this hypothesis. In both populations, the intraspecific K2P distance was lower than 1% and the interspecific K2P distance was 19.9%, showing a large barcode gap (Borges *et al.* 2012). This level of divergence is much higher than the average interspecific divergence in molluscs (8-16%) (Hebert *et al.* 2003) and comparable to the average interspecific divergence of 21.7% and 17.5% in heteropod and pteropod gastropods, respectively (Radulovici *et al*. 2010). For 18S rRNA gene sequences, the K2P distance between northeast Atlantic and eastern Mediterranean populations of 0.3% was much lower than that in COI sequences. It was, however, similar to the K2P distance between distinct teredinid species such as *L. pedicellatus* and *Bankia carinata* (Gray, 1827) (0.3%) and *L. pedicellatus* and *L. massa* (Lamy, 1923) (0.3%) (Borges *et al*. 2012). The divergence in COI and 18S rRNA gene sequences between northeast Atlantic and eastern Mediterranean populations of the morphospecies *L. pedicellatus* also indicate that no detectable genetic exchange exists between these populations and that this situation has been stable over a long period of time (Borges *et al.* 2012).

The arguably most important aspect of the discovery of a new species is its description following standardized conventions in the International Comission on Zoological Nomenclature (ICZN 1999). In recent years, the use of molecular data as the primary or sole source of data in species descriptions has increased and has been increasingly accepted by the taxonomic community (e.g. Jörger & Schrödl 2013; Félix *et al.* 2014; Wang *et al.* 2016). This is particularly important in the case of cryptic species, for which molecular data may be key to species recognition. In this context, the molecular character-based model (DeSalle *et al.* 2005) provides discrete molecular diagnostic characters within DNA sequences that are particularly useful for the diagnosis of cryptic species (Jörger & Schrödl 2013). They can be used as diagnostic features, in a similar fashion as traditional morphological diagnostic features are used for species diagnosis (Bergmann *et al.* 2009). Furthermore, molecular diagnostic characters from type material used to diagnose new taxa make the type material even more valuable for future research. This is because types are usually better preserved in museum collections than in private collections (Renner 2016).

To test the hypothesis of a new species, our candidate *Lyrodus mersinensis* **sp. nov.**, referred to as *L. pedicellatus* Mediterranean form (Borges *et al.* 2012), we analysed the barcode index numbers (BINs) for the putative new species and *L. pedicellatus* publicly available in the Barcode of Life Data System (BOLD System) (Ratnasingham & Hebert 2007). In addition, we used sequences of 28S rRNA gene publicly available in the National Centre for Biotechnology Information (NCBI) (Taylor *et al.* 2007; Distel *et al.* 2011; Weigelt *et al.* 2016) to test the results obtained by Borges *et al*. (2012) with COI and 18S rRNA gene sequences. Finally, we determined molecular diagnostic characters from three independent molecular markers (COI, 18S rRNA, and 28S rRNA genes) to formally describe *L. mersinensis* **sp. nov.** and redescribe *L. pedicellatus*. The aim is to improve `taxonomic resolution´ in this species complex because many studies rely on taxonomic precision. Examples include studies of species diversity, one of the most widely adopted measures of biodiversity (Chiarucci *et al*. 2011), biogeography (Borges *et al*. 2014a) and bioassessment (Lenat and Resh 2001; Chessman *et al*. 2007).

Material and methods

Collection and identification of specimens. Specimens of *Lyrodus mersinensis* **sp. nov.** were collected in 2007 from panels of Scots pine, *Pinus sylvestris* L., exposed in Mersin Bay, Turkey, the type locality. Specimens of *L. pedicellatus* were collected in 2008 and 2009 along the Atlantic coast of France (Table 1, Figure 1). For detailed methodology see Borges *et al.* (2012). In addition, all specimens were identified to species level when the pallets were present, following Turner (1966; 1971). Specimens that did not possess pallets were identified only to family level (Teredinidae) and later identified to species level based on their DNA barcodes (Borges *et al.* 2012). The morphology of pallets from specimens of *L. mersinensis* **sp. nov.** was compared to that of pallets of specimens identified morphologically as *L. pedicellatus*, collected in the same area (Mersin, Turkey) and in Rovinj, Croatia from the work of Borges (2014). They were also compared with specimens of *L. pedicellatus* obtained from several locations in France (Borges *et al.* 2012), England and Portugal (Borges 2014), and with a photomicrograph of of the neotype of *L. pedicellatus* provided by the Muséum National d´Histoire Naturelle in Paris, France. All

specimens were imaged and ancillary data were collected. Images and metadata are publicly available in the BOLD System project "Wood Boring Mollusca from Europe" (WBEM). The types are deposited at the Muséum National d´Histoire Naturelle. All other specimens and dissected pallets are stored at the Helmholtz-Zentrum Geesthacht, Germany, for future reference.

TABLE 1. Species (as in sequences downloaded from GenBank), collection area, accession numbers and source of all sequences used in the analysis.

Species	Collection area	GenBank accession numbers				Source
		COI	short 18S	Long 18S	28S	
B. carinata	Mersin, Turkey	KC157914; KC157934	KC158195; KC158213			Borges *et al*. 2012
B. carinata	Bonaire			JF899203	JF899175	Distel *et al*. 2011
B. carinata	Tobago			AF120564		Giribet & Wheeler 2002
L. pedicellatus	Toulindac, France	KC157917-KC157920	KC158198-KC158201	KU201120; KU201121; KU201122	KU201129	Borges *et al*. 2012; Weigelt *et al*. 2016
L. pedicellatus	Gulf of Morbihan, France	KC157915; KC157921; KC157922	KC158196; KC158202; KC158203			Borges *et al*. 2012
L. pedicellatus	Berder, France	KC157937	KC158216			Borges *et al.* 2012
L. pedicellatus	Portsmouth, UK			AM774540	AM779714	Taylor *et al*. 2007
L. pedicellatus	Florida, USA			JF899211	JF899184	Distel *et al*. 2011
L. mersinensis	Mersin, Turkey	KC157916; KC157932; KC157938; KC157939	KC158197; KC158211; KC158217; KC158218	KU201123	KU201127	Borges *et al*. 2012; Weigelt *et al*. 2016
N. norvagica	Penerf, France	KC157924	KC158205		KU201128	Borges *et al*. 2012; Weigelt *et al.* 2016
N. norvagica	Berder, France	KC157925	KC158206			Borges *et al.* 2012
N. norvagica	Mersin, Turkey	KC157926-KC157931; KC157936	KC158207-KC158210; KC158214; KC158215	KU201117; KU201118; KU201119		Borges *et al*. 2012; Weigelt *et al.* 2016
N. norvagica	Kaş, Turkey	KC157923; KC157933	KC158204; KC158212			Borges *et al*. 2012
T. navalis	Mersin, Turkey			KU201114; KU201115; KU201116	KU201126	Weigelt *et al.* 2016
T. navalis	Belfast, Maine, USA			JF899222	JF899194	Distel *et al*. 2011
T. dominicensis	Antalya, Turkey	KC157940-KC157943	KC158219-KC158222	KU201124; KU201125	KU201130	Borges *et al*. 2012; Weigelt *et al*. 2016
T. dominicensis	Bonaire			JF899225	JF899197	Distel *et al*. 2011

Test of the hypothesis of *Lyrodus mersinensis* sp. nov. To more robustly test the hypothesis of a new species in the *Lyrodus pedicellatus* species complex in Europe, we analysed the BIN report provided by the BOLD System; BINs had not yet been implemented in the BOLD system at the time of the publication of Borges *et al.* (2012). The rationale for BINs stems from the similarity criterion, where divergence in COI rarely exceed 2% within a named species, whereas divergence between species is typically higher, more than 4% divergence from their nearest neighbour, the `barcode gap´ (Hebert *et al.* 2003; 2004). The BIN algorithm examines the correspondence between

specimens identified to species level through prior taxonomic work and those of species inferred from the analysis of COI sequence variation. The method uses a new algorithm (RESL) to cluster records with high sequence similarity and connectivity and separates those with lower similarity and sparse connectivity (Ratnasingham & Hebert 2013).

As a second line of evidence, we used 28S rRNA gene sequences publicly available in the NCBI (see Table 1 for details). First, we analysed whether *L. mersinensis* **sp. nov.** and *L. pedicellatus* showed reciprocal monophyly in this gene using the ML method. Then, we determined their interspecific K2P distances to compare with those obtained by Borges *et al.* (2012) from COI and 18S sequences. This was done because the agreement between data obtained from several independent genes is valuable evidence to support the existence of two independent evolutionary lineages (Knowlton 2000).

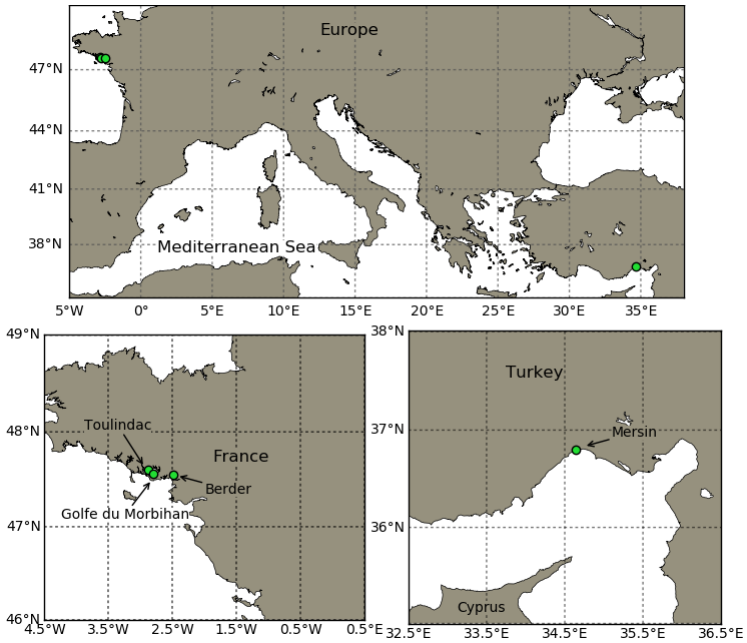

FIGURE 1. Location of sample sites of *Lyrodus pedicellatus* and *Lyrodus mersinensis* **sp. nov.** sequenced. Location details are given in Table 1.

Molecular diagnostic characters used for diagnosis. Sequences of the mitochondrial gene COI (~658bp), the nuclear genes 18S rRNA (~345 bp and ~1700bp), and 28S rRNA (~1300bp) were obtained from the NCBI (details and accession numbers in Table 1). Multiple alignments were generated for the three markers individually using "Muscle" (Edgar 2004), "Clustal W" (Larkin *et al*. 2007) both implemented in "MEGA" v. 6.1 (Tamura *et al.* 2013) and "Geneious" v. 10.9 (Kearse *et al*. 2012), to determine which algorithm produced the most conservative and reliable alignments. This was an essential step for quality control because the homology assumption between sequences is crucial for the correct detection of molecular diagnostic characters (Jörger & Schrödl 2013). In addition, COI sequences were translated into amino acids to check for the presence of pseudogenes (numts), stop codons or unusual amino acid sequence patterns in the alignments. The amino acid sequences were also used to determine molecular diagnostic characters in *L. pedicellatus* and *L. mersinensis* **sp. nov.**

The COI alignments (both nucleotides and amino acids) produced by the three software algorithms were identical. In 18S (longer and shorter sequences) and 28S, "Muscle" produced the most conservative alignments. Therefore, the alignments produced by "Muscle" were chosen to select the diagnostic molecular characters, which include only "pure single characters" (present in all members of a taxon, but absent in all members of other taxa), according to the methodology described in Jörger & Schrödl (2013). Position 1 in each alignment refers to the first nucleotide after removing the primer regions (as downloaded from the NCBI). In the diagnosis of the new species, the reference sequences (COI, short and long 18S, and 28S) were retrieved from the holotype.

For COI (both nucleotides and amino acids), sequences of *L. mersinensis* **sp. nov.** were compared to those of *L. pedicellatus* (sister species), *Nototeredo norvagica* (Spengler, 1792), *Bankia carinata* and *Teredothyra dominicensis* (Bartsch, 1921). The 18S (long and shorter) and 28S sequence of *L. mersinensis* **sp. nov.** were

compared with sequences of the same species analysed in COI and also with sequences of *Teredo navalis* Linnaeus, 1758, from the work by Weigelt *et al.* (2016). We could not compare the COI sequences of *L. mersinensis* to sequences of other *Lyrodus* species because there are no available COI sequences of other species in this genus. Sequencing other species in *Lyrodus* was beyond the scope of the present work.

We also determined molecular diagnostic characters to redescribe *L. pedicellatus* using the same procedure. We did not include members of the families Xylophagidae or Pholadidae to avoid the risk of including homoplastic characters which increases with evolutionary distance (Rach *et al* 2008). This is particularly the case in fast evolving markers such as COI. In order to carry out the DNA comparisons efficiently, we developed a software tool in Python, FastaChar. The source code and manual, both released under the GPLv3 license, are available for download from https://github.com/smerckel/fastachar.

Results

Morphological comparison of pallets. The comparison of the pallets from eastern Atlantic and Mediterranean populations with pallets of specimens obtained by Borges (2014) from several European sites shows that all pallets have the typical morphology of *L. pedicellatus* as in Turner (1971) (Figs. 2, 3). Thus, the genetic divergence in COI and 18S rRNA genes reported by Borges *et al.* (2012) has no parallel in the morphology of the pallets.

Barcode Index Numbers. The analysis of the BIN report produced by the BOLD system (as of the 1st of October 2017) showed that COI sequences of specimens identified morphologically as *Lyrodus pedicellatuss* were split into two concordant BINs. One BIN (BOLD: AAO8110) includes all specimens collected in Mersin, Turkey, and the other (BOLD: AAU1654) includes all specimens collected on the Atlantic coast of France (for locations see Table 1).

Molecular analysis of 28S rRNA sequences. The ML phylogram produced using the 28S rRNA gene sequences separated all species lineages present in the dataset, including *L. mersinenis* **sp. nov.** and *L. pedicellatus* This confirms the reciprocal monophyly between *L. mersinensis* **sp. nov.** and *L. pedicellatus* (Fig. 2) shown in the phylograms of COI and 18S rRNA genes (Borges *et al.* 2012). Without exception, the pairwise distances of 28S were considerably smaller than the COI distances and larger than those of the 18S sequences (Table 2). In 28S sequences, the K2P distance between *L. mersinensis* **sp. nov.** and *L. pedicellatus* was 1.5% whereas K2P distances in COI and 18S sequences for the two species were 19.9% and 0.3%, respectively.

TABLE 2. Pairwise 28S for teredinid groups using K2P distances (%). Sequences from specimens belonging to the *Lyrodus pedicellatus* complex were divided into three subgroups, one from the Mediterranean (*L. mersinensis* **sp. nov.**), one from the Atlantic (`true´ *L. pedicellatus*) and the last from Florida (probably *L. floridanus*).

Taxon	Pairwise distances					
	1	2	3	4	5	6
1- *Lyrodus pedicellatus* Mediterranean form						
2- *Lyrodus pedicellatus* Atlantic form	1.53					
3- *Lyrodus pedicellatus* Florida, USA	4.45	3.88				
4- *Nototeredo norvagica*	11.62	11.63	12.02			
5- *Teredo navalis*	2.86	2.86	4.12	11.11		
6- *Teredothyra dominicensis*	11.59	11.68	12.69	10.07	10.71	
7- *Bankia carinata*	6.44	6.26	6.11	10.49	5.78	10.64

Molecular diagnostic characters. The morphological comparison between pallets of specimens of *Lyrodus mersinensis* **sp. nov.** and *L. pedicellatus* did not reveal reliable characters for diagnosing the two species. Thus the description of *L. mersinensis* sp. nov and redescription of *L. pedicellatus* are based on molecular diagnostic characters, pure single characters, in DNA sequences of mitocondrial COI and nuclear 28S.

Sequences of nuclear 18S did not yield molecular diagnostic characters either for *L. mersinensis* sp. nov or for *L. pedicellatus*. Tables 3 and 4 show a unique combination of diagnostic nucleotides obtained from COI and 28S,

respectively, for *L. mersinensis* **sp. nov.** Tables 4 and 5 show the positions in COI and 28S DNA sequences, respectively, with diagnostic nucleotides for *L. pedicellatus*. COI sequences provide more molecular diagnostic characters for both species than 28S sequences.

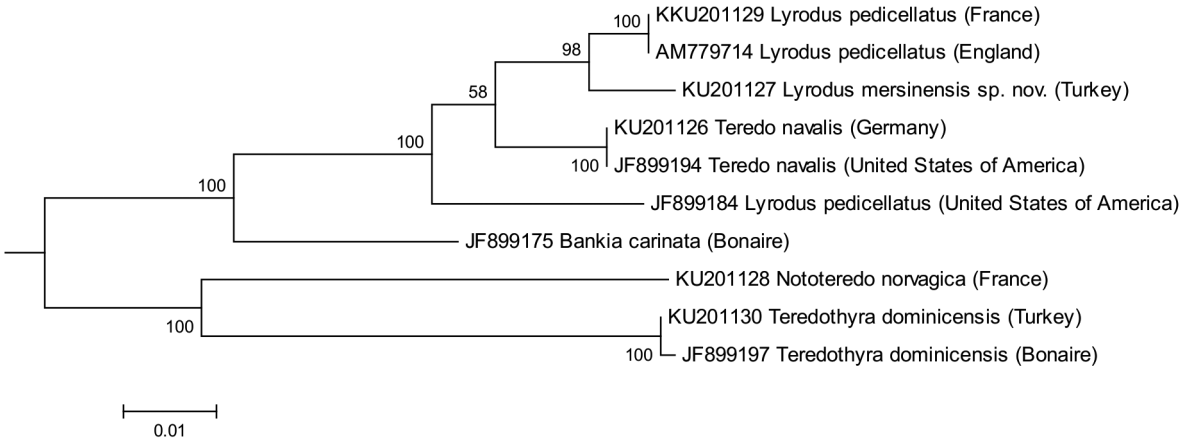

FIGURE 2. Maximum-likelihood phylogram based on partial sequences of the 28S rRNA gene obtained from GenBank showing accession numbers. Numbers associated with nodes represent bootstrap values greater than 50. Scale bar indicates 0.01 substitutions per site.

Discussion

Delineation of species in the *Lyrodus pedicellatus* complex in Europe. In many taxa, speciation has not been accompanied by morphological differentiation even though the entities are genetically isolated, the so-called cryptic species (Knowlton 2000). In the last two decades, the discovery of cryptic species across taxonomic groups has increased dramatically with the use of molecular techniques, such as the barcode region (COI) proposed by Hebert *et al.* (2003). Borges *et al.* (2012) presented strong evidence for the existence of a cryptic species pair in the morphospecies *Lyrodus pedicellatus* in Europe. The two populations of this morphospecies were reciprocally monophyletic and showed a deep divergence (barcode gap) of 19.9% in COI. In studies derived from barcode initiatives, the barcode gap has become the method of choice for delineation of species (e.g. Hebert *et al.* 2004; Puillandre *et al.* 2012; Sanders *et al.* 2017). In many studies based on COI sequences only, algorithms such as the Automatic Barcode Gap Discovery (ABGD) (Puillandre *et al.* 2012) and the General Mixed Yule Coalescent (GMYC) (Pons *et al*. 2006) are helpful in estimating confidence levels of species hypotheses in cases where there are less character data to build the diagnosis on than in species separated by 4 % of COI divergence or more (Ratnasingham & Hebert 2013).

Nevertheless, we further corroborate the hypothesis that *Lyrodus mersinensis* merits recognition as a new species by using two additional sources of evidence, BINs and sequences of another independent nuclear gene (28S) available in the NCBI. In addition, the number of molecular diagnostic characters in these species, derived from COI and 28S rRNA genes, makes it highly unlikely that these characters fall within the range of variation of another species (see below). The split of the specimens identified morphologically as *L. pedicellatus* (prior to barcoding) in two separate concordant BINs (i.e. a BIN that includes only one species) further corroborates the hypothesis of cryptic species in what had been considered a single species, *L. pedicellatus*on from the Atlantic and Mediterranean coasts of Europe. Furthermore, the reciprocal monophyly for *Lyrodus mersinensis* **sp. nov.** and *L. pedicellatus* (with 98% bootstrap support) in the 28S ML phylogram (Fig.1) is in line with that observed in the COI and 18S phylograms in the study by Borges *et al.* (2012). The 1.5% K2P distance between *L. mersinensis* **sp. nov.** and *L. pedicellatus* is also congruent with values observed for other species in this gene, much lower than in COI and higher than in 18S (e.g. Romano *et al*. 2014). As discussed by Borges *et al.* (2012), it is more reasonable to assume that the populations from the Atlantic coast of France are the `true´ *L. pedicellatus* described from the Atlantic coast of Spain, and the population from the Mediterranean is a new cryptic species, *L. mersinensis*.

TABLE 3. Molecular diagnostic characters from COI sequences of *Lyrodus mersinensis* **sp. nov.** (bold) compared to, *Nototeredo norvagica*, *L. pedicellatus*, *Bankia carinata*, and *Teredothyra dominicensis*. Numbers in parenthesis refer to the number of sequences from each species used in the analysis. No intraspecific divergence was found in any of these positions in the species examined. The two sequences of *Bankia carinata* were shorter (656 bp) and the dash means no information.

Marker: COI-5P	**Molecular diagnostic characters**				
Position	***L.* mersinensis (4)**	*N.norvagica* (11)	*L. pedicellatus* (8)	*B. carinata* (2)	*T. dominicensis* (4)
61	**C**	G	T	G	A
67	**T**	A	G	G	C
106	**G**	T	A	A	T
112	**G**	A	C	A	T
142	**G**	A	A	A	A
199	**C**	A	A	A	A
202	**C**	T	T	T	T
208	**G**	A	A	A	T
251	**C**	T	T	T	T
304	**C**	T	T	T	T
319	**C**	T	T	T	T
382	**A**	G	T	T	T
400	**G**	T	T	T	C
409	**G**	T	A	A	T
463	**G**	A	A	T	A
475	**T**	G	A	G	G
478	**T**	C	A	A	G
481	**T**	A	A	G	G
493	**G**	T	T	A	T
499	**A**	T	T	C	C
526	**G**	T	T	T	A
538	**T**	A	A	G	G
550	**A**	G	G	G	G
553	**G**	A	T	T	T
557	**C**	T	T	T	T
559	**T**	A	A	A	G
565	**T**	G	G	G	G
571	**G**	A	A	A	T
610	**C**	T	T	T	T
619	**G**	A	T	T	C
652	**C**	T	T	T	T
658	**C**	T	T	-	T

Molecular diagnostic characters. Until recently, the use of molecular data as the primary or the sole source of data for describing species was uncommon (Cook *et al*. 2010). This has been a contentious area with many taxonomists and non-taxonomists skeptical of the validity of using molecular data to diagnose or to describe species, resulting in the rejection of manuscripts describing new species and exacerbating the problems in alpha taxonomy. However, there is no compelling evidence to exclude descriptions using molecular data as the primary data for diagnosing species. Indeed, using alternative kinds of data for description should not pose a problem for taxonomy when the descriptions are linked to the type specimens (Cook *et al.* 2010) as established by the ICZN (1999). A species diagnosis based on molecular diagnostic characters is founded on a well-established hypothesis

that character differences reflect lineage independence. In addition, the use of molecular diagnostic characters satisfies Article 13.1.1 of ICZN (1999) just as morphological characters do (Bauer *et al*. 2011). In cryptic species, in particular, morphological characters are not an adequate proxy for species boundaries. Thus, molecular diagnostic characters might be more informative and practical, which was the case in *Lyrodus mersinensis* **sp. nov.** Therefore, we chose to use molecular diagnostic characters from three independent markers (two of them informative) to diagnose *L. mersinensis* **sp. nov.** and to provide a new diagnosis for *L. pedicellatus*, according to the method proposed by Jörger & Schrödl (2013).

It could be argued that information regarding reproductive strategy/length of parental care, used for instance by Calloway & Turner (1983) to distinguish *Lyrodus floridanus* from *L. pedicellatus* is of taxonomic value. Although we agree that such data are taxonomically valuable, it requires breeding of specimens in laboratory conditions to obtain the relevant data on reproductive strategy and length of parental care. In future research in this area, it appears unlikely that this method will be used in routine identification of unknown specimens. In many studies, teredinid specimens are extracted incomplete or die during extraction from test panels or from fixed wooden structures exposed in the marine environmen, but the fresh tissue can be preserved. Thus, sequence data, that are easy to obtain nowadays, can be used to identify unknown teredinid specimens in a straightforward manner, and at a fraction of the time and cost required to breed specimens in the laboratory.

Choice of markers to describe teredinids. Description of species should be based on markers that show a level of interspecific variability to enable the discrimination of recently evolved species, and a lower intraspecific variability to allow specimens to be assigned to species (Jörger & Schrödl 2013). Of the three markers examined in this study, COI (nucleotides) was the one which provided most of the distinctive characters between *Lyrodus mersinensis* **sp. nov.** and *L. pedicellatus*. This was to be expected because substitution rates in nucleotides in mitochondrial genes are, in general, higher than those in nuclear rRNA genes (Raupach *et al*. 2010). Nevertheless, 28S sequences also contain unique diagnostic characters to distinguish between the two cryptic species which confirms previous results that the 28S rRNA gene is a good marker to discriminate species in the Teredinidae (Taylor *et al*. 2007; Distel *et al*. 2011; Weigelt *et al.* 2016). In contrast, the translated amino acids (COI) did not yield diagnostic characters. This is because amino acid sequences are usually more conserved than nucleotide sequences.

The 18S rRNA gene sequences (short and long) did not yield unique molecular characters for either of the two species. A number of studies have reported that 18S has a limited ability to discriminate among recently diverged species (Raupach *et al*. 2010) which is in line with our results for the compared teredinids. Nonetheless, the multi-marker barcode approach used herein represents an effective method for the delineation and description of cryptic species in the Teredinidae because, as pointed out by Jörger & Schrödl (2013), at least two of the markers used were informative. In addition, the use of multi-marker approach insures that the diagnosis is not hampered by mtDNA introgression from one species to another.

Distribution of *Lyrodus pedicellatus*. The morphospecies *Lyrodus pedicellatus* has been reported to occur worldwide (Turner 1966; Turgeon *et al*. 2009; Borges *et al*. 2014). However, in some cases such as *L. pedicellatus* from California larvae are unlikely to be dispersed widely by ocean currents because of their short planktonic phase ranging from few hours to three days (Pechenik *et al.* 1979; Calloway & Turner 1988). Dispersal by driftwood or ships has been long recognised as playing a role in the distribution of this morphospecies (Turner 1966). Rafting adults in driftwood can be transported by currents, particularly after extreme events such as tsunamis (Carlton *et al*. 2017) or storms. Little experimental work has been done, however, to test whether adult teredinids in driftwood can survive and reproduce successfully during rafting. It was hypothesised that algal-boring limnoriids are able to reproduce successfully during rafting (Miranda & Thiel, 2008), but this has been shown neither for wood-boring limnoriids or for teredinids (Borges *et al*. 2014b). In addition, the open ocean presents a nearly impassable barrier to most wood-boring species (Voight, 2015). During historical times, the transport of adult teredinids in the hulls of wooden ships is thought to have been important in the distribution of many teredinid species (Carlton 1985; 1999; Carlton & Hodder 1995). Nowadays, this type of transport has no impact in the distribution of teredinids as few wooden vessels exist. Nevertheless, ships are still important vectors in the distribution of teredinids. Larvae have been found in ballast water (Gollasch 2002), and larvae and adults in pieces of wood may be transported in sea-chests (protected areas built in the hull of ships below the waterline) (Borges *et al.* 2014b). In the case of *L. pedicellatus* from the Atlantic, the larvae are able to settle immediately after being released (Lebour 1946) and, thus, are very effective at colonising wood in new environments.

In temperate and tropical seas, transport of species mediated by human activity is likely to have obscured the original range of many teredinid species (Voight 2015), including the morphospecies *Lyrodus pedicellatus*. Before human activity, however, rafting adults may have played a determinant role not only for distribution but also gene flow between populations of this morphospecies. Nevertheless, it is also possible that oceanographic barriers may have constrained gene flow between populations in geographically distant areas over large time scales. Indeed, there is evidence that the specimen from Florida identified as *L. pedicellatus* by Distel *et al*. (2011) is *L. floridanus* (Borges *et al*. 2012; Weigelt *et al*. 2016) and *L. pedicellatus* from California, also identified by Distel *et al.* (2011) and considered by Calloway & Turner (1988) as the `true´ *L. pedicellatus*, is a fourth cryptic species in the *L. pedicellatus* complex (Weigelt *et al*. 2016, Fig. 2). In addition, we argue that it is possible that more cryptic species exist in this morphospecies. This hypothesis is worth testing but is, however, beyond the scope of the present work.

Conclusions

The taxonomy of the Teredinidae, like that of many other groups, would benefit from comprehensive and carefully curated reference libraries of DNA barcodes, where each species is linked to an array of DNA sequences (Costa & Antunes 2012) and also molecular diagnostic characters from at least two informative markers. The use of DNA sequences represents a promising and effective tool for accurate identification and description of species in the Teredinidae. This is particularly important for species such as *Lyrodus floridanus* that cannot be distinguished morphologically from its sister species *L. pedicellatus* (Calloway & Turner 1988). Presently, their distinction requires knowledge on their respective brooding time and the stage at which the larvae are released into the plankton; this knowledge is unavailable in routine identifications. As a consequence, specimens of these species are either not identified to species level or possibly misidentified creating confusion in the literature. This situation can be easily overcome by sequencing specimens from species that are suspected to be cryptic, in order to identify them.

Systematics

Teredinidae Rafinesque, 1815

Lyrodus Gould, 1870

Lyrodus mersinensis sp. nov. Borges & Merckelbach

Fig. 3

Synonymy. *Lyrodus pedicellatus* Mediterranean form (Borges *et al.* 2012), *L. pedicellatus* II (Weigelt *et al.* 2016), *Lyrodus pedicellatus* Turkey (Treneman *et al.* 2018).

Type material. Holotype: specimen with pallets (MNHN IM-2000-33821); BOLD ID: WBET133, project "Wood Boring Mollusca from Europe", publicly available in the BOLD System; DNA voucher stored deep frozen (-80ºC) at the University of Minho, Braga, Portugal. Paratypes: three specimens (MNHN IM-2000-33822, MNHNIM-2000-33823, MNHN-IM-2000-33824); BOLD IDs: WBET130; WBET134; WBET135. All specimens were collected at the type locality, preserved in 96% ethanol and stored at 4ºC at the Institute for Coastal Research, Helmholtz-Zentrum Geesthacht, Germany. The types are deposited at the Muséum National D´Histoire Naturelle in Paris, France.

Type locality. Mersin Bay, Mersin, Turkey (36º N 48´; 36º E 38.4´); Mediterranean Sea.

Other material examined. Morphology of the pallets of specimens obtained by Borges (2014) from Mersin, Turkey (n = 127) and Rovinj, Croatia (n = 301).

Morphological diagnosis. The morphologic characters are identical to those of *Lyrodus pedicellatus* (see below) according to Turner (1966; 1971).

Molecular diagnosis. COI sequences yield 32 molecular diagnostic characters between position 61 and position 658 (Table 3). 28S rRNA sequences yield eight molecular characters in positions 111(T), 112(T), 450(G), 708(T), 714(C), 759(A), 1248(T), and 1262(G) (Table 4). BIN BOLD: AAO8110 (n = 4), including the holotype. Intraspecific variation: 0.4%; closest neighbour species: *Bankia carinata* at a genetic distance of 19.3% and *Lyrodus pedicellatus* at a genetic distance of 19.9%.

Etymology. Named after the type locality, Mersin, south of Turkey.

Distribution. Currently known only from the type locality, but probably widespread in the Mediterranean and possibly the Black Sea (Borges *et al*. 2014a).

Habitat. Marine; wood-boring organisms.

TABLE 4. Molecular diagnostic characters from 28S rRNA gene sequences of *Lyrodus mersinensis* **sp. nov.** (bold) compared to sequences of *L. pedicellatus, Nototeredo norvagica*, *Teredo navalis*, *Teredothyra dominicensis*, and *Bankia carinata*. Numbers in parenthesis refer to the number of sequences from each species used in the analysis. Indels (insertions or deletions) in sequences of *Nototeredo norvagica* and *Teredothyra dominicensis* are indicated as dashes.

Marker: 28S	**Molecular diagnostic characters**					
Position	***L. mersinensis* (1)**	*L. pedicellatus* (3)	*N. norvagica* (1)	*T. navalis* (2)	*T. dominicensis* (2)	*B. carinata* (1)
111	**T**	A/G	C	G	G	A
112	**T**	C	A	C	A	C
450	**G**	T	A	C	C	C
708	**T**	C	A	C	C	C
714	**C**	T	-	T	-	G
759	**A**	G	G	G	G	G
1248	**T**	C	C	C	G	A
1262	**G**	C	C	C	C	C

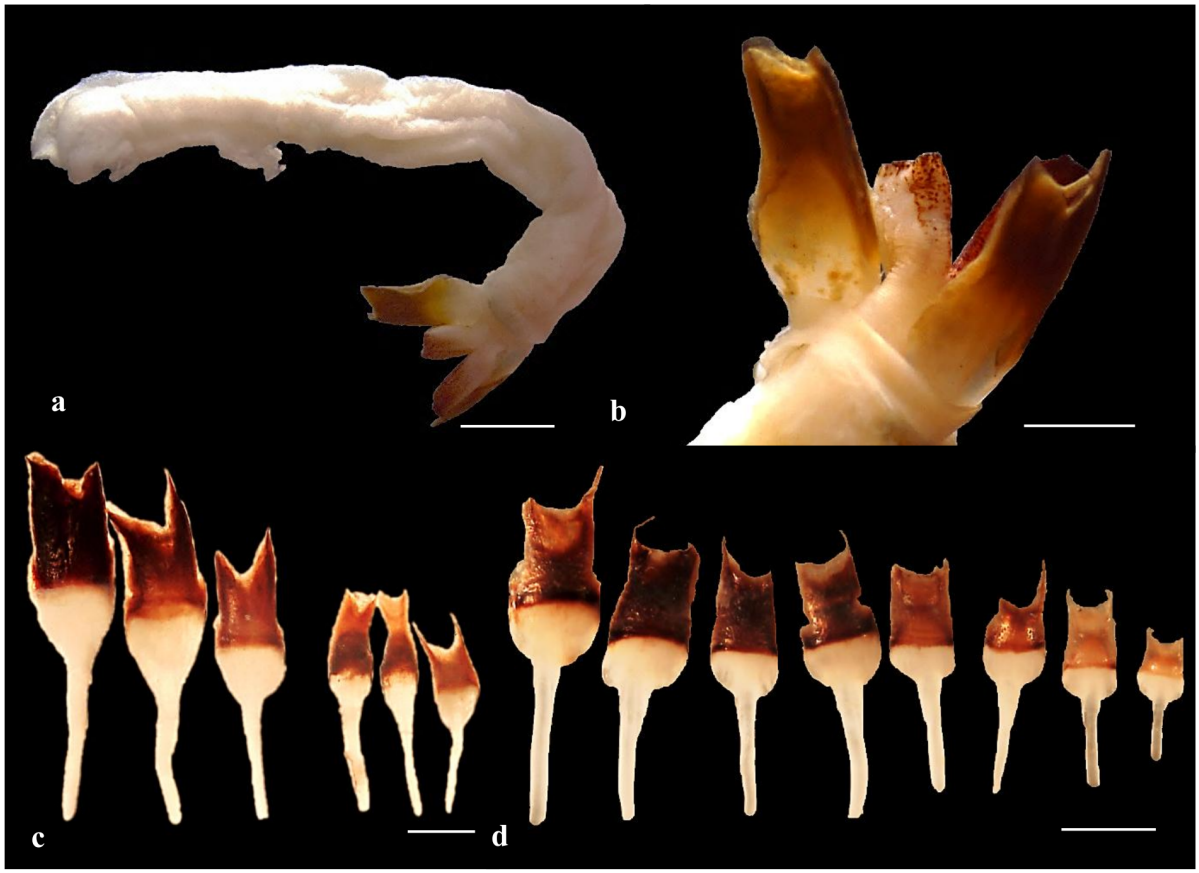

FIGURE 3. *Lyrodus mersinensis* **sp. nov.** (a, b) and selected dissected pallets of specimens of the same species used for comparison from the work by Borges (2014) (c, d). (**a**) body lacking the anterior end and the shell; (**b**) detail of pallets showing the distal portion of the blade with conical shape and periostracum characteristic of *pedicellatus*-like *Lyrodus*; (**c**) Mersin, Turkey; (**d**) Rovinj, Croatia. Scale bars 2 mm.

***Lyrodus pedicellatus* (Quatrefages, 1849)**
Figs. 4, 5

Synonymy. *T. dalli* Moll & Roch, 1931.
Teredo arabica Roch, 1935 (?), *T. calmani* Roch, 1931 (?), *T. chlorotica* Gould, 1870 (?), *T. dagmarae* Roch, 1931 (?), *T. diegensis* Bartsch, 1916 (?), *T. franziusi* Roch, 1929 (?), *T. hawaiensis* Dall, Bartsch & Rehder, 1938 (?), *T. helleniusi* Moll, 1936 (?), *T. hibicola* Kuronuma, 1931 (?), *T. honoluluensis* Edmondson, 1946 (?), *T. indica* Nair, 1958 (?), *T. kauaiensis* Dall, Bartsch & Rehder, 1938 (?), *T. lamyi* Roch, 1929 (?), *T. linaoana* Bartsch, 1927 (?), *T. lomensis* Roch, 1929 (?), *T. madraensis* Nair, 1956 (?), *T. malaccana* Roch, 1935 (?), *T. midwayensis* Edmondson, 1946 (?), *T. nodosa* Roch, 1929 (?), *T. pertingens* Iredale, 1932 (?), *T. pochhammeri* Moll, 1931 (?), *T. robsoni* Roch, 1931 (?), *T. samoaensis* Miller, 1924 (?), *T. siamensis* Bartsch, 1927 (?), *T. taiwanensis* Taki & Habe, 1945 (?), *T. tateyamensis* Kuronuma, 1931 (?), *T. togoensis* Roch, 1929 (?), *T. townsendi* Bartsch, 1922 (?), *T. tristi* Iredale, 1936 (?), *T. yatsui* Moll, 1929 (?).

Type material. The types are unkown (Moll 1941). A neotype was selected by Moll (1941) from Quatrefages´ collection in the Muséum National d´Histoire Naturelle (MNHN-IM-2000-32924) and although not marked, Turner (1966) considered it to be the neotype selected by Moll (1941) because it was the only specimen with pallets from the type locality.

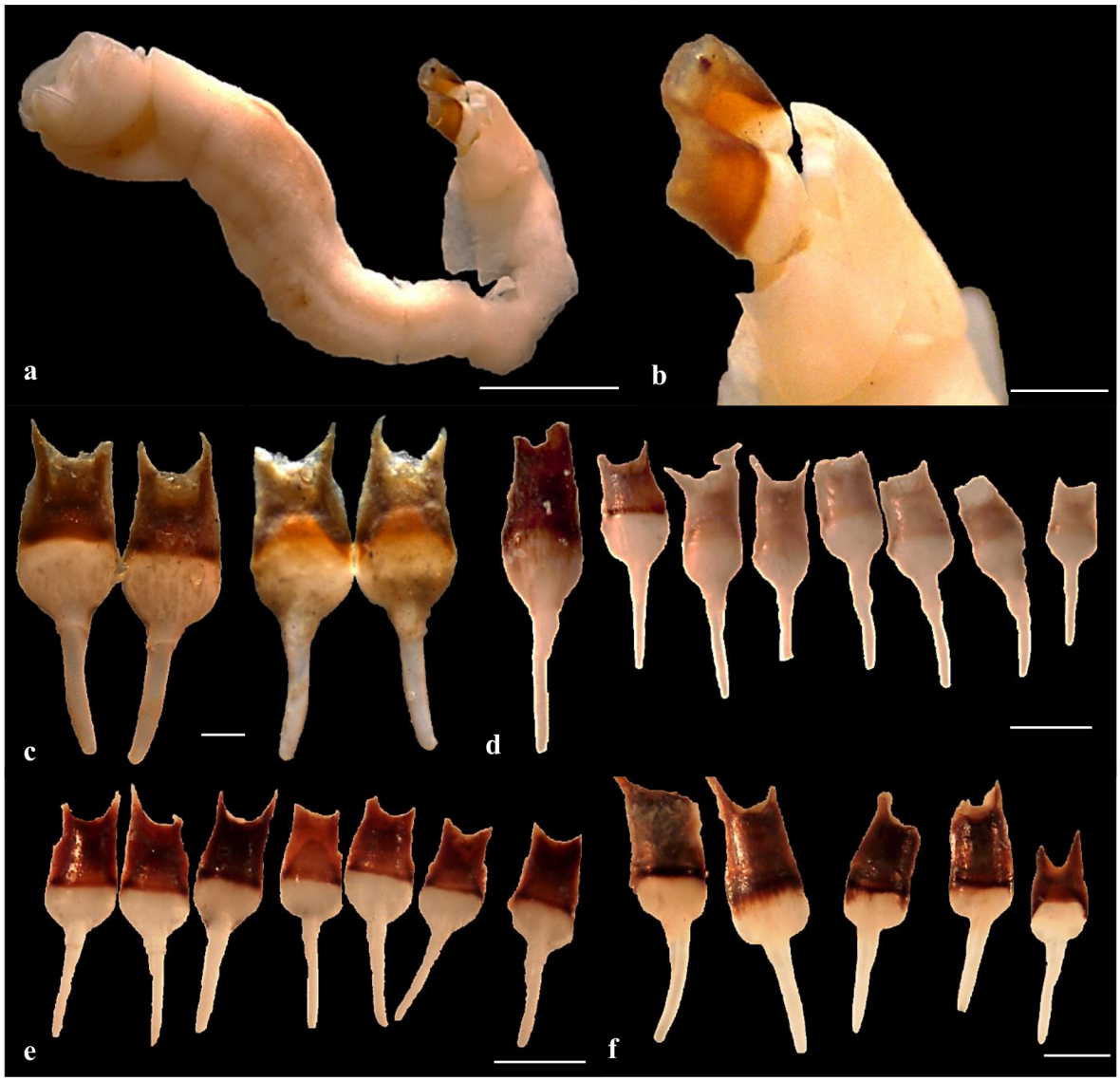

FIGURE 4. *Lyrodus pedicellatus* from Brittany, France (**a, b**) and selected dissected pallets of specimens of the same species used for comparison from the work by Borges (2014) (**c–f**). (**a**) full body; (**b**) detail of pallets showing the distal portion of the blade with conical shape; (**c**) pallet pair from Portsmouth, UK, outer face (left), inner face showing the distal portion of the blade with conical shape (right); (**d**) series of different-sized pallets from Portsmouth, UK; (**e**) Olhão, Portugal; (**f**) Azores, Portugal. All pallets have the characteristics of the morphospecies *L. pedicellatus*. Scale bars (a, b, d, e and f) 2 mm; (c) 1 mm.

TABLE 5. Molecular diagnostic characters from COI-5P gene sequences of *Lyrodus pedicellatus* (bold) compared to those of *L. mersinensis* **sp. nov.**, *Nototeredo norvagica*, *Teredothyra dominicensis*, and *Bankia carinata*. Numbers in parenthesis refer to the number of sequences used in the analysis.

Marker: COI-5P	**Molecular diagnostic characters**				
Position	***L.pedicellatus* (8)**	*L.mersinensis* (4)	*N. norvagica* (11)	*B. carinata* (2)	*T. dominicensis* (4)
19	**A**	T	T	T	T
22	**A**	T	T	T	T
34	**A**	T	T	T	T
38	**C**	T	G	T	A
43	**A**	T	T	G	G
46	**A**	T	T	G	T
52	**G**	A	T	A	T
55	**A**	G	G	G	G
61	**T**	C	G	G	A
64	**A**	G	G	G	G
112	**C**	G	A	A	T
121	**A**	G	T	G	C
130	**A**	T	T	T	T
214	**G**	A	A	A	T
217	**A**	T	T	G	T
268	**A**	G	T	G	T
316	**A**	T	T	T	C
328	**G**	T	T	T	T
335	**T**	C	C	C	G
337	**G**	T	C	A	T
412	**A**	T	T	T	C
415	**A**	G	T	G	T
448	**C**	T	A	T	A
466	**A**	G	G	G	G
472	**A**	T	G	T	T
475	**A**	T	G	G	G
502	**A**	G	G	G	G
520	**T**	A	A	G	A
529	**C**	G	A	G	A
547	**A**	T	T	T	T
625	**T**	C	A	C	G
626	**C**	T	T	T	T
628	**T**	A	G	G	A
640	**A**	G	G	G	G

Type locality. Pasajes Port, San Sebastian, Spain (43º N 19´; 1º W 54´); Atlantic Ocean.

Material examined. Pallets of the specimens barcoded by Borges *et al.* (2012) were compared with pallets of *Lyrodus pedicellatus* obtained by Borges (2014) from Portsmouth, England (n= 210); Terceira, Azores, Portugal (n= 341); and Olhão, Portugal (n= 231). In addition, they were compared with pallets of *Lyrodus mersinensis* **sp. nov.** (see details above) and with the neotype, using a high-quality micrograph provided by the Muséum National d´Histoire Naturelle, Paris, France (Fig. 5).

FIGURE 5. *Lyrodus pedicellatus* (Quatrefages, 1849). Neotype (broken specimen from San Sebastian, Spain, the type locality) at the Muséum National d´Histoire Naturelle, Paris. View of the specimen in different positions. Left: first- ventral position; second- dorsal position; third- lateral position; fourth-lateral position. Right: view of each pallet. Photomicrograph by Manuel Caballer MNHN, project E-RECOLNAT: ANR-11-INBS-0004. Scale bar 4 mm.

TABLE 6. Molecular diagnostic characters from 28S rRNA gene sequences of *Lyrodus pedicellatus* (bold) compared to those of *L. mersinensis* sp. nov., *L. pedicellatus, Nototeredo norvagica*, *Teredo navalis*, *Teredothyra dominicensis*, and *Bankia carinata*. Numbers in parenthesis refer to the number of sequences used in the analysis. Tk—Turkey; Bn—Bonaire; Fr—France; Gr—Germany; US—United States of America.

Marker: 28S	**Molecular diagnostic characters**								
Position	***L. pedicellatus* (2)**	*L. mersinensis* Tk (1)	*L. pedicellatus* Bn (1)	*N. norvagica* Fr (1)	*T. navalis* Gr (1)	*T. navalis* US (1)	*T. dominicensis* Tk (1)	*T. dominicensis* Bn (1)	*B. carinata* Bn (1)
463	**T**	C	C	A	C	C	C	C	C
586	**T**	C	C	C	C	C	C	C	C
719	**T**	G	G	G	G	G	G	G	G

Morphological diagnosis. Pallets non-segmented. Calcareous portion of blade composed of a single thick piece, distally conical. Distal half of the blade composed by a loose-fitted periostracum, more or less straight-sided, sometimes extending as lateral horns; distal margin concave to U-shaped. Periostracum varying from light brown to nearly black (Turner 1971).

Molecular diagnosis. COI sequences yield 34 molecular diagnostic characters between position 19 and position 640 (Table 5). 28S rRNA sequences yield three molecular characters in positions 463(T), 586 (T), 719(G) (Table 6).

Distribution. Reported as occurring worldwide (Turner 1966; Turgeon *et al.* 2009; Borges *et al.* 2014a).

Habitat. Marine; from the intertidal to depths down to 37m (Turgeon *et al.* 2009); wood-boring organisms.

The present article is registered at ZooBank (www.zoobank.org), under the ZooBank Life Science Identifiers

(LSIDs) (urn:lsid:zoobank.org:pub:8EDAD8DB-413B-495B-8879-E6D3D020F30C) to comply with the requirements of the ICZN (1999).

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