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ORIGINAL ARTICLE

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The phylogeny of the genus *Indoplanorbis* (Gastropoda, Planorbidae) from Africa and the French West Indies

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Abstract

Indoplanorbis exustus is a freshwater snail known as the intermediate host of various trematode parasites, including different species of the genus *Schistosoma*. Although its genetic diversity is well described in Asia, the phylogenetic diversity of strains from Africa and Guadeloupe (French West Indies) and their relationship to Asian and South-East Asian strains remain unknown. To tackle this issue, we sampled individuals from Africa and Guadeloupe, and we computed phylogenetic reconstructions using five molecular markers: partial sequences of two mitochondrial genes, cox1 and 16S, and three nuclear markers, ITS1, ITS2 (Internal Transcribed Spacer 1 and 2) and 5.8S. Our results suggest that strains in Africa and Guadeloupe come from Asia and that they all belong to a single clade that is widespread around the globe.

1 | INTRODUCTION

*Indoplanorbis exustu*s (Deshayes, 1834) is a freshwater gastropod of the Planorbidae family, known as the only species within the *Indoplanorbis* genus. In the field, the morphology of the shell is very close to other planorbid freshwater snails such as *Biomphalaria pfeifferi* (Krauss, 1848) and *Helisoma duryi* (Wetherby, 1879), and only the fine examination of the reproductive system makes it possible to discriminate between them. *Indoplanorbis exustus* is known to be widely distributed in South Asia (India, Bangladesh, Nepal, Sri Lanka, Pakistan) and South-East Asia (Indonesia, Philippines, Vietnam, Laos, Malaysia, Thailand, Myanmar). However, its presence has also been reported in East Asia (Japan; [http://www.env.go.jp/en/nature/as/041110.pdf] in 2004), the Middle East (Oman: Wright & Brown, 1980); Yemen (Socotra Island: Wright, 1971), Africa (Ivory Coast: Mouchet, Rey, & Cunin, 1987); (Nigeria: Kristensen & Ogunnowo, 1987); (Benin: Ibikounlé, Massougbodji, Sakiti, Pointier, & Moné, 2008) and French West Indies (Guadeloupe: Pointier, David, & Jarne, 2005).

Three main phylogenetic studies have been conducted on *I. exustus* using various samples from Asia (Sri Lanka, India, Nepal, Bangladesh), South-East Asia (Indonesia, Philippines, Vietnam, Laos, Malaysia, Thailand, Myanmar) and from the Middle East (Oman). These analyses were computed using different genes, including mtDNA Cox1 and mtDNA 16S (Devkota, Brant, & Loker, 2015; Gauffre-Autelin, von Rintelen, Stelbrink, & Albrecht, 2017; Liu et al., 2010). All studies showed the presence of four genetically distinct clades with a strong phylogenetic divergence between them, suggesting that *I. exustus* is a complex of several species. However, no study investigated the genetic diversity of *I. exustus* from Africa and French West Indies. To address this gap, we sampled *I. exustus* gastropods in both geographic regions, and we compared their nucleotide sequences with previously described strains from Asia and South-East Asia.

2 | MATERIAL AND METHODS

2.1 | Sampling, DNA extraction, amplification and sequencing

All *I. exustus* specimens were collected in the field (Supporting information Appendix 1). DNA from 70 specimens was extracted: Vietnam (two specimens from one site), Malaysia (one specimen from Parit Jawa and three specimens from Batu Kajak), Thailand (two specimens from Khanom West and two from Hat Samila), Bangladesh (five specimens), Oman (five specimens from Wadi Tiwi and five from Wadi Shab), Gabon (five specimens), Benin (five specimens from each of the following sites: Acron, Djassin, Tchivié, Asecna and Pahou (five waterbodies all located in the South of Benin, not far from the capital Porto Novo) and Parakou, Ivory Coast (five specimens) and Guadeloupe in the French West Indies (four specimens from Mare-à-boire and one from Séo). *Bulinus globosus* from Benin was used as outgroup (five specimens). The specimens were stored in 90% ethanol. The snail head-foot region was ground manually using a Pellet Pestle blue polypropylene (Merck). Total DNA was extracted using the E.Z.N.A. Tissue DNA Kit (Omega Bio-tek, USA) according to the manufacturer's protocol.

The partial sequences of two mitochondrial genes cox1 and 16S and three nuclear markers ITS1, 5.8S and ITS2 were amplified by PCR using previously published primers (see Supporting information Appendix 2). Sequencing was performed by GATC Biotech (Konstanz, Germany) using forward and reverse primers. GenBank accession numbers are reported in Appendix 1 (Supporting information), according to each gene.

2.2 | Phylogenetic analyses

The data set for this study was complemented with sequences published by four research groups (Table 1). DNA multiple sequence alignments were performed according to codons or nucleotides using MUSCLE program on the MEGA software (Edgar, 2004; Tamura, Stecher, Peterson, Filipski, & Kumar, 2013). Poorly aligned and highly variable region alignments were automatically removed using GBlocks 0.91b (Castresana, 2000; Dereeper et al., 2008; Dereeper, Audic, Claverie, & Blanc, 2010; http://molevol.cmima.csic.es/castresana/Gblocks_server.html) to allow for the following three options: smaller final blocks, gap positions within the final blocks and less strict flanking positions for "Codons" or "Nucleotides" sequences.

TABLE 1 Number of specimens of *Indoplanorbis exustus* used for phylogenetic analyses

	Cox1	16S	ITS1_5.8S	ITS2
Present study	70	70	70	70
Albrecht, Kuhn, and Streit (2007)	1	—	—	—
Liu et al. (2010)	13	13	—	—
Devkota et al. (2015)	30	31	17	—
Gauffre-Autelin et al. (2017)	53	—	—	—
Total	167	114	87	70

Phylogenetic trees were obtained via Bayesian inference (BI) and maximum-likelihood (ML) methods. In BI analyses, coding DNA sequences were partitioned according to codon position and the estimation of model parameters was unlinked across partitions. For noncoding DNA, reversible-jump MCMC was used to sample over the space of all possible substitution models of the GTR family (see Huelsenbeck, Larget, & Alfaro, 2004). Bayesian analyses were carried out with MRBAYES v3.2 (Ronquist et al., 2012), with four chains of 2,000,000 generations (except for ITS2: 3,000,000 generations), trees sampled every 200 generations (except for ITS2: 300 generations) and burnin value set to 20% of the sampled trees. We checked that standard deviation of the split frequencies fell below 0.01 to ensure convergence in tree search. In ML analyses, different models of DNA evolution (for coding or noncoding sequences) and associated parameters were estimated using IQ-TREE v1.3.8 (Nguyen, Schmidt, von Haeseler, & Minh, 2015) and the best parameters were identified based on the Bayesian Information Criterion (BIC). ML trees were then computed with IQ-TREE v1.3.8 using the best model and validated via an ultrafast bootstrap procedure with 1,000 replicates (Minh, Nguyen, & von Haeseler, 2013). All trees were built using haplotypes according to each country of sampling only, that is when the same haplotype was found in two different countries, we considered one haplotype for each country.

2.3 | Nucleotide divergence

The haplotypes were selected using the percentage of differences calculated from the estimates of evolutionary divergence between sequences (matrix of pairwise distances) obtained using MEGA 6.06 software (Tamura et al., 2013).

3 | RESULTS

3.1 | Phylogenetic relationships

BI and ML methods revealed congruent topologies within and between markers. Therefore, we show only below the BI tree with posterior probabilities and bootstrap values from ML analyses for mtDNA Cox1. The phylogenetic relationships for mtDNA 16S, nuclear DNA ITS1_5.8S and ITS2 are presented in Appendix 3 (Supporting information). The results of the 582 bp Cox1 analysis conducted on 167 specimens revealed the presence of 46 haplotypes. The phylogenetic tree (Figure 1) shows the presence of four differentiated clades of *I. exustus* designated A–D. Among the 70 new specimens used in the present study, 14 haplotypes were found. All of them belonged to clade D, except for our five Bangladeshi specimens that showed five haplotypes and were assigned to clade C. All the specimens from South-East Asia belonged to clade D, except those from Laos that were assigned to clades C and D. They shared clade D with some Asian haplotypes from India, Sri Lanka and Nepal. The 12 specimens from Oman showed three haplotypes, two in the same waterbody (Wadi Shab) and one in two other waterbodies (Wadi Bani Khalid and Wadi Tiwi). The Guinea Gulf specimens used in this study (five from Gabon, 30 from Benin, corresponding to six locations, and five from Ivory Coast) shared a unique haplotype which was identical to the Batu Kajak and Borneo Malaysian haplotype. The Guadeloupean specimens exhibited two haplotypes, very close to the haplotype from Sri Lanka (the percentages of difference were 0.23% and 0.47% for Séo and Mare-à-boire, respectively) and more distant from the other members of clade D, with differences that reach 4.12% with the Indian and Nepalese haplotypes. At last, specimens from Nepal were very diverse, as they corresponded to the four clades of *I. exustus*.

3.2 | Nucleotide divergences

The estimates of evolutionary divergence between Cox1 sequences showed that the percentages of intraclade differences (between 0 and 5.33%) were lower than interclade differences (between 7.39% and 14.09%) (Table 2), suggesting that these four clades are different phylogenetic groups. These percentages were similar to those between each clade and the outgroup *Bulinus*. The estimates of the nucleotide divergence between 16S, ITS1-5.8S and ITS2 sequences are presented in Appendix 4 (Supporting information).

To compare with *I. exustus* data, we quantified the nucleotide divergence between several species of *Bulinus* (Basommatophoran snails, Planorbidae) which has 37 species divided into four groups (*Bulinus africanus* group [10 species], *Bulinus forskalii* group [11 species], *Bulinus reticulatus* group [two species] and *Bulinus truncatus/tropicus* group [14 species]). The analysis was computed using a 1009-bp-long multiple alignment of 17 nucleotide sequences (Supporting information Appendix 5). Similarly to *I. exustus*, estimates of evolutionary divergence between Cox1 sequences showed that the percentages of intraclade differences (from 0.79% to 11.00%) were lower than interclade differences (from 12.09% to 15.36%) (Table 3).

4 | DISCUSSION

The present work is a continuation of previous studies on the phylogenetic relationships of *I. exustus* with new samples, never studied before, originating both from common regions in the continental Asia and South-East Asia, and in particular from expansion zones such as Guinea Gulf in Africa and Guadeloupe in French West Indies. Phylogenetic trees, based on two mitochondrial genes (Cox1 and 16S), showed congruent results with four main clades such as observed by Devkota et al. (2015). According to the Cox1 and 16S data, the first three clades (A–C) consist mainly of samples originating from continental Asia (India, Nepal, Bangladesh), with the exception of samples from Laos and Myanmar. Similarly to the analysis of strains from Nepal (Devkota et al., 2015), our results suggest that the genetic diversity of *I. exustus* is very high for India, Bangladesh, Laos and Myanmar.

Considering the very high level of genetic divergence between the four clades ranging from 7.39% to 14.09% for the Cox1 and from 2.34% to 10.07% for the 16S, *I. exustus* is probably a complex of cryptic species such as it was proposed by Liu et al. (2010), Devkota et al. (2015) and Gauffre-Autelin et al. (2017). These percentages are similar to what was obtained for different species of *Bulinus* and could be an argument for the existence of several species within *Indoplanorbis*.

Although the four clades of *I. exustus* do not show morphological differences in the shell, a thorough morphological study of the reproductive system (Supporting information Appendix 6) would likely highlight significant morphological differences. A similar morphological study of the reproductive system of *H. duryi* and *I. exustus* (Ibikounlé et al., 2008) allowed for the separation of the two species. For *I. exustus*, we would expect to see significant differences between clades with respect to the prostatic gland (mainly their diverticulates) and the penial complex (bulinid type) with its penis sheath and the preputium. At last, the Nepal strains are ideal candidate for this study since the four clades are found in this country.

The presence of different populations of *I. exustus* far from their native region (Asia and South-East Asia) in the

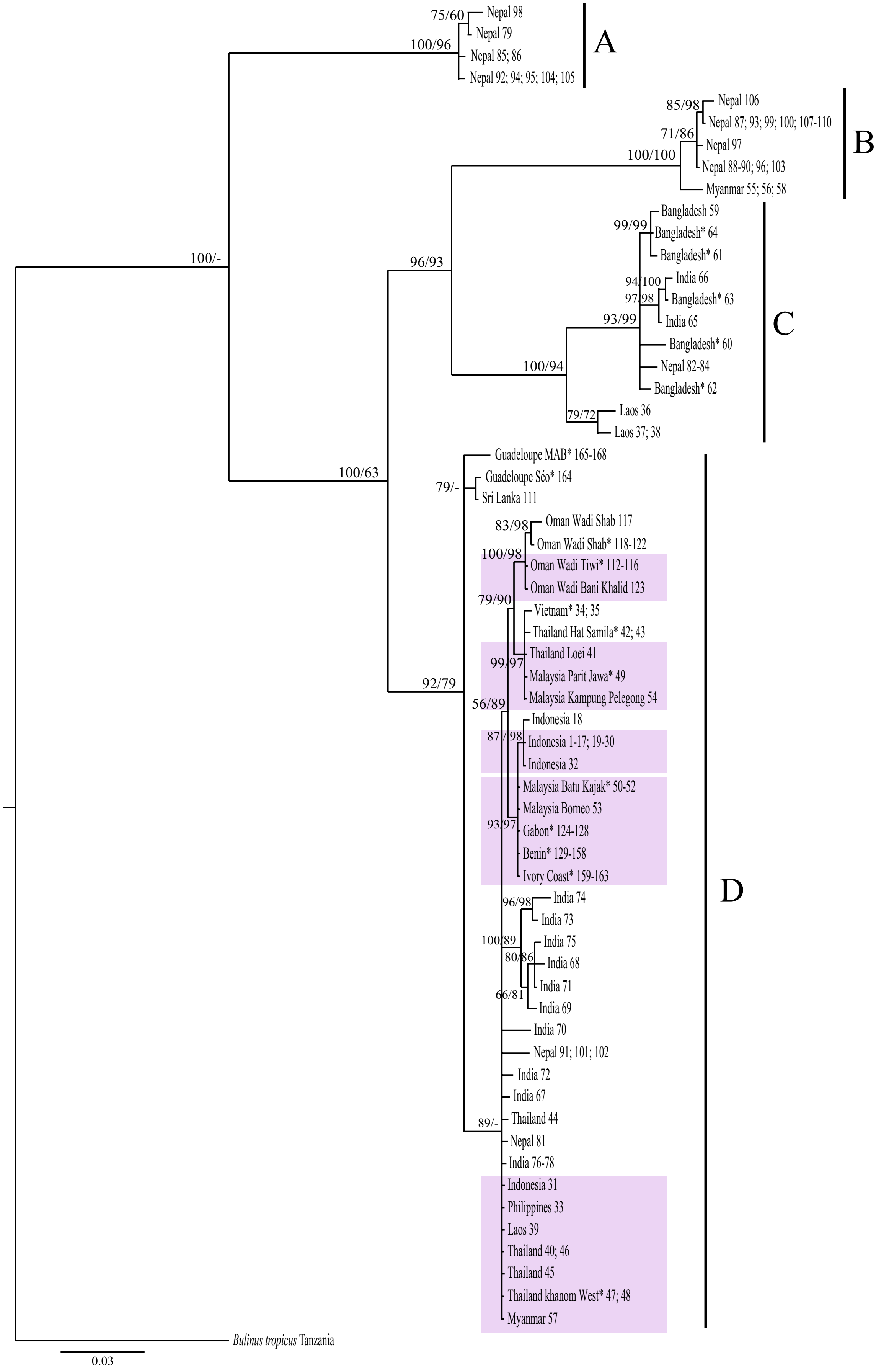
75/60
Nepal 98
Nepal 79
100/96
Nepal 85; 86
Nepal 92; 94; 95; 104; 105
A
85/98
Nepal 106
Nepal 87; 93; 99; 100; 107-110
71/86
Nepal 97
100/100
Nepal 88-90; 96; 103
Myanmar 55; 56; 58
B
Bangladesh 59
99/99
Bangladesh* 64
Bangladesh* 61
100/-
96/93
94/100
India 66
97/98
Bangladesh* 63
India 65
93/99
C
Bangladesh* 60
100/94
Nepal 82-84
Bangladesh* 62
Laos 36
79/72
Laos 37; 38
Guadeloupe MAB* 165-168
100/63
Guadeloupe Séo* 164
79/-
Sri Lanka 111
83/98
Oman Wadi Shab 117
Oman Wadi Shab* 118-122
100/98
Oman Wadi Tiwi* 112-116
Oman Wadi Bani Khalid 123
79/90
Vietnam* 34; 35
Thailand Hat Samila* 42; 43
Thailand Loei 41
99/97
Malaysia Parit Jawa* 49
92/79
Malaysia Kampung Pelegong 54
56/89
Indonesia 18
87/98
Indonesia 1-17; 19-30
Indonesia 32
Malaysia Batu Kajak* 50-52
Malaysia Borneo 53
93/97
Gabon* 124-128
Benin* 129-158
Ivory Coast* 159-163
D
96/98
India 74
India 73
100/89
India 75
80/86
India 68
India 71
66/81
India 69
India 70
Nepal 91; 101; 102
India 72
India 67
Thailand 44
89/-
Nepal 81
India 76-78
Indonesia 31
Philippines 33
Laos 39
Thailand 40; 46
Thailand 45
Thailand khanom West* 47; 48
Myanmar 57
Bulinus tropicus Tanzania
0.03

FIGURE 1 Bayesian inference tree of *Indoplanorbis exustus* based on mitochondrial cytochrome oxidase I sequences. This analysis was computed using a 582-bp-long multiple alignment of 61 nucleotide sequences, including the outgroup (*Bulinus tropicus*). The samples with an asterisk are those collected in this study. Each group of highlighted samples constitutes a unique haplotype. Node supports are indicated by Bayesian posterior probabilities and by the maximum-likelihood bootstrap values. Numbers after taxa origins corresponded to the location numbers of Appendix 1 (Supporting information)

TABLE 2 Estimates of evolutionary divergence between Cox1 sequences (intra [diagonal] and interclades [shaded]). Numbers indicate percentage of difference and correspond to minimal and maximal values of *p*-distance

	Clade A	Clade B	Clade C	Clade D
Clade A	0.34–1.03			
Clade B	11.34–12.37	0.17–0.69		
Clade C	12.03–14.09	9.11–10.82	0.17–5.33	
Clade D	11.86–13.57	9.28–11.86	7.39–10.14	0–4.12
Outgroup *Bulinus tropicus*	Min = 13.92		Max = 15.81	

TABLE 3 Estimates of evolutionary divergence between Cox1 sequences (intra [diagonal] and interclades [shaded]). Numbers indicate percentage of difference and correspond to minimal and maximal values of *p*-distance. The analysis was made on 17 species of *Bulinus* belonging to three different groups (Supporting information Appendix 4)

	B. africanus group	*B. forskalii* group	*Bulinus truncatus/tropicus* group
B. africanus group	1.19–11.00		
B. forskalii group	12.09–15.36	1.29–10.90	
B. truncatus/tropicus group	12.39–14.37	12.10–14.60	0.79–4.56

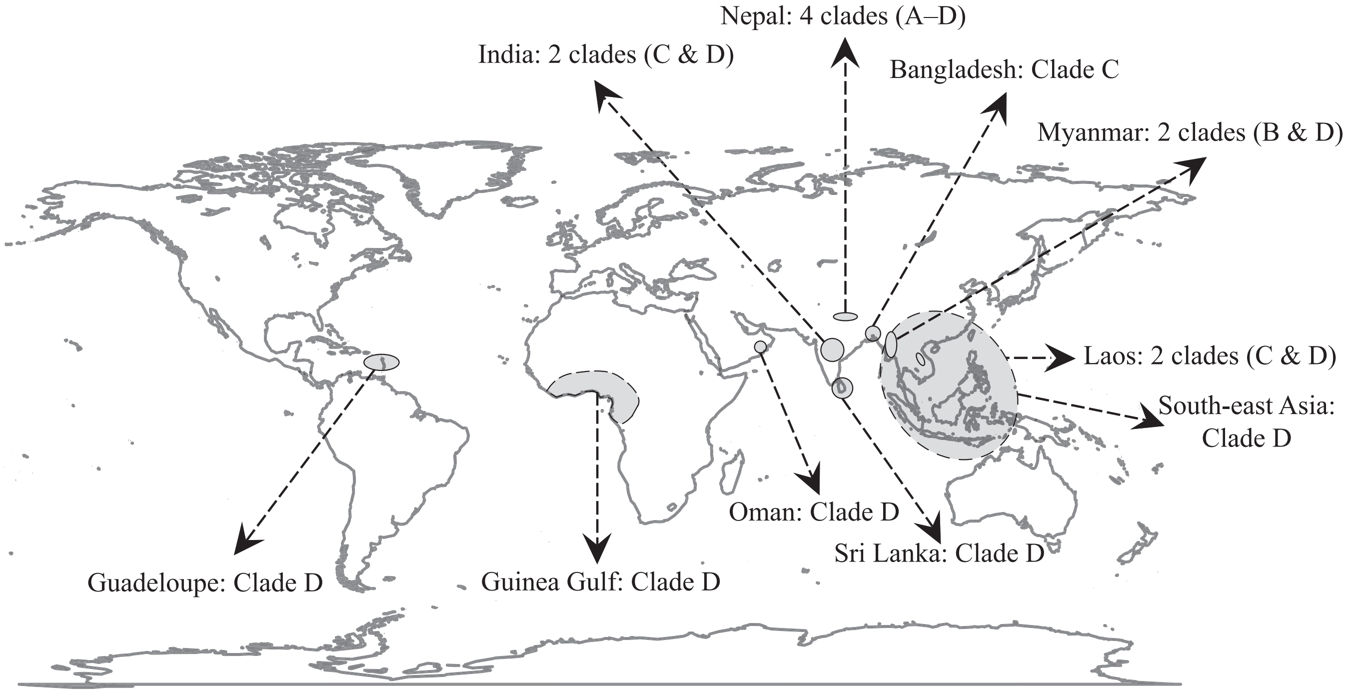

FIGURE 2 Global geographical distribution of *Indoplanorbis exustus* clades according to the Bayesian and maximum-likelihood phylogeny using Cox1 and 16S mitochondrial genes

Guinea Gulf (Africa) and in Guadeloupe (Caribbean region) raises the question of their origin (Figure 2). The results of the phylogenetic reconstructions showed that all the samples collected in the Guinea Gulf are identical and constitute a single haplotype, whereas the east–west distance between Libreville (Gabon) and Agboville (Ivory Coast) was about 1,637 km (as the crow flies) and the largest distance between the two farthest Beninese localities was nearly 420 km on the south–north axis (Cotonou-Parakou). The African haplotype is assigned to clade D for the Cox1 and 16S with a large number of samples originating from India, Nepal, Sri Lanka, South-East Asia, Oman and Guadeloupe. The samples collected in Guadeloupe originating from two localities (MAB and Séo) separated only by 17 km (as the crow flies) showed two different haplotypes belonging to the clade D for Cox1 and 16S. This could suggest two different introduction events. Overall, our analysis suggests that the presence of *I. exustus* in Africa and French West Indies resulted from the geographic expansion of a single clade (D), originally located in Asia.

The presence of *I. exustus* far from its "original" geographic region is possibly linked to commercial activities that have intensified in recent decades (Pointier et al., 2005). Human activities are known to transport a fairly large number of species to areas outside their native range (Williamson, 1996). For example, *H. duryi* originated from North America and expanded into South America and Africa (Pointier et al., 2005).

The geographical expansion is probably facilitated by the high self-fertilisation capacity of *I. exustus* (Bony et al., 2013 and Escobar et al., 2011) and may have important parasitological implications as it is the natural intermediate host of four species of schistosomes belonging to the genus *Schistosoma* (*S. indicum*, *S. nasale, S. spindale* and *Schistosoma* sp.) and at least one avian schistosome (Devkota, Brant, Thapa, & Loker, 2014; Devkota et al., 2015). Indeed, when the vector of a parasitosis is present in a geographical area, nothing excludes the emergence of the disease if the parasite is introduced. This happened recently in France (Corsica) where *B. truncatus* is present in different waterbodies and allowed for the transmission of *S. haematobium* likely linked to the arrival of migrants from West Africa where Bilharziasis is endemic (Boissier et al., 2016; Holtfreter, Moné, Müller-Stöver, Mouahid, & Richter, 2014; Moné et al., 2015). As *I. exustus* is the intermediate host of several species of *Schistosoma*, nothing excludes the emergence of *I. exustus*-transmitted livestock Bilharziasis in Africa.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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