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1 **Hitchhiking freshwater clams: First report of *Sphaerium nucleus* attached to**  
2 ***Lissotriton helveticus* in France**

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10 Phoresy is a specific form of commensalism where a mobile organism affords transport to a  
11 less mobile one (White, Morran, & de Roode, 2017). Many phoretic associations have been  
12 described (Clausen, 1976; Binns, 1982; Bartlow & Agosta, 2021) of which several examples  
13 involve freshwater molluscs; presumably because they have limited ability to make long  
14 distance dispersal by themselves. Charles Darwin (1882) made pioneering observation of such  
15 dispersal in the freshwater mussel *Unio complanatus* attached to the toe of a duck, as well as  
16 supposedly *Sphaerium corneum* (then named *Cyclas cornea*) caught on the toes of newts  
17 (species not defined). Since then, multiple studies have reported phoretic associations  
18 between freshwater bivalves and lizards (Lopez et al., 2005), frogs and toads (Kolenda et al.,  
19 2017), and newts (Audibert et al., 2013).

20 Among amphibians, newts appear to be often used as 'hosts' by freshwater mussels  
21 for two reasons. First, mussels can attach easily to the toes of newts whereas attaching to the  
22 skin folds of anurans is more difficult (Kolenda et al., 2017). Second, newt species may move  
23 between ponds during breeding season (Denoël et al., 2018) which would facilitate local

24 mussel dispersal (Lopez et al., 2005). Accordingly, multiple studies have described examples  
25 of different newt species carrying small freshwater mussels of the genus *Sphaerium*. For  
26 instance, *Sphaerium corneum* has been found attached on the toes of *Lissotriton helveticus*  
27 (Laza-Martínez et al., 2012; Audibert et al., 2013), *Triturus marmoratus* (Boissinot & Migault,  
28 2016), *Ichthyosaura alpestris* (Audibert et al., 2013), and *Sphaerium nucleus* was found to be  
29 attached to *Lissotriton helveticus* and *Triturus cristatus* (Wood et al., 2008). The frequency of  
30 this phenomenon may differ widely between sites. For example, a study in Luxembourg, very  
31 high mussel densities were found at one site of around 3000 per m<sup>2</sup>, where 23% of the 161  
32 captured newts had *Sphaerium nucleus* or *Pisidium obtusale* attached to their toes while  
33 occurrence was less frequent at two other sites where mussel attachment to newt toes was  
34 recorded on 3.6% and 7% of newts (Wood et al., 2008).

35 In this study, we report the observation of *Sphaerium nucleus* attached to the toes of *L.*  
36 *helveticus*. We sampled newts on 15 April 2022 around 23:00 h in two small forest ponds  
37 (France; 0° 25' 27.85'' W, 46° 8.0' 49.56'' N, 0° 25' 29.28'' W, 46° 8.0' 4 5.24'' N, 70m a.s.l) of  
38 about 26 and 75 m<sup>2</sup> respectively. In addition to *Lissotriton helveticus*, we observed (but not  
39 capture) *Rana dalmatina* and *Alytes obstetricans* in Pond 1, and *Triturus marmoratus*, *Triturus*  
40 *x blasii*, *Bufo spinosus*, *Rana dalmatina*, *Alytes obstetricans* and *Pelophylax esculentus* in Pond  
41 2. The two ponds host several aquatic plant species. In pond 1, we captured 37 *L. helveticus*  
42 individuals (21 females and 16 males), out of which 8 individuals (21.6 % of individuals, 5  
43 females and 3 males) presented clams attached to their toes (see Figure 1), and 13 presented  
44 wounds to their toe (35.1% individuals, 8 females and 5 males). Clams were attached to the  
45 toes of forelegs (4 females and 2 males) and hind legs (1 female and 1 male). All individuals  
46 had only one clam attached. In pond 2, we caught 69 *L. helveticus* individuals (57 females and  
47 12 males). Surprisingly, while this pond was situated a hundred meters from the first pond

48 and free living mussels have been seen at the bottom, we did not find clams attached to *L.*  
49 *helveticus* toes.

50 Freshwater clams clamped onto newt toes were collected and subsequently identified  
51 as belonging to the *Sphaerium corneum* group, within which it is sometimes difficult to assign  
52 a species name based on morphological characters alone. The specimens sampled exhibited a  
53 general shell shape intermediate between *Sphaerium corneum* (Linnaeus, 1758) and *S. nucleus*  
54 (Studer, 1820). However, the high porosity of the shells and the size and shape of the hinge  
55 teeth allowed these specimens to be assigned to *S. nucleus* (Kořínková, Beran, & Horsák,  
56 2008).

57 To our knowledge, this is the first report of *Sphaerium nucleus* attached to *L. helveticus*  
58 in France although this clam species has been observed attached to *L. helveticus* in  
59 Luxembourg (Wood et al., 2008). In the same geographic area of our observation (6 km from  
60 our study sites), the closely related *S. corneum* was found on larger newt species (e.g.,  
61 Boissinot & Migault, 2016), while in other parts of France, and Spain, *S. corneum* has been  
62 found on *L. helveticus* (Laza-Martínez et al., 2012; Audibert et al., 2013). Such observations  
63 highlight the fact that both *Sphaerium* species can attach to different newt species, regardless  
64 of their size. However, we emphasize the complex identification of species from the  
65 *Sphaerium corneum* group which also include a third species, *S. ovale* (Férussac, 1807), whose  
66 taxonomic validity is still debated (Prié et al., 2021). The morphologic similarities of these taxa  
67 may obscure the identification of, but also the true diversity of, the freshwater clam species  
68 involved in these phoretic interactions.

69 Our report suggests that phoresy may be site specific. Indeed, this phenomenon can  
70 either be rare (Audibert et al., 2013) or frequent (Wood et al., 2008) within a population and

71 with variations between sites (Wood et al., 2008). The observed differences between the two  
72 ponds in the frequency of mussel attachment to newts may be explained by the density of the  
73 mussel populations (a parameter we did not assess) and of the presence of other amphibian  
74 species.

75 'Host' selection by phoretic bivalves, if any, still needs to be explored. Indeed, Boissinot  
76 & Migault (2016) have shown that in a pond where *L. helveticus*, *T. cristatus*, and *T.*  
77 *marmoratus* co-occurred, only *T. marmoratus* was affected, despite the fact that *L. helveticus*  
78 and *T. cristatus* were more abundant. This suggests that 'host' selection may occur, a process  
79 for which chemical orientation of the phoront has already been assessed to play a role in frog  
80 and lizard 'hosts' (Lopez et al., 2005). Wood et al. (2008) suggest alternatively that newt  
81 species behaviours and habitat use, or simply toe size and structure, must also impact the  
82 likelihood of attachment of sphaerid mussels. As mussel attachment can cause damage to  
83 individuals toes (Wood et al., 2008), this makes the relationship appear to be parasitic,  
84 because the mussels benefits by being facilitated in dispersal while the newts are harmed.  
85 Indeed, such damage may interfere with oviposition (Wood et al., 2008) and eventually reduce  
86 newts displacements; however these potential disadvantages are likely to be temporary as  
87 newts are capable of limb regeneration (Scadding, 1981).

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131 **Figure 1.** *Sphaerium nucleus* found on a female *Lissotriton helveticus*, in a pond in the Deux-Sèvres  
132 department

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