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A molecular genetic approach showed no difference between American and French specimens of *E. compressa* as well as Dutch individuals of *E. casertana f. plicata*, confirming the presence of this North-American pea clam species in The Netherlands. The analysis of this species in various collections revealed that *E. compressa* was introduced into Northeastern Germany before 1940, probably via the Elbe estuary and the Hamburg harbour. The apparent extension of the species over Western Europe since the 1990s suggests a second phase of introduction.

Key words: pea clams, Sphaeriidae, *Euglesa compressa*, North America, Western Europe, France, alien.

**Introduction**

Abnormal specimens of *Euglesa casertana* (Poli, 1791), formerly *Pisidium casertanum*, identified by Kuiper, were observed in the Brandenburg-area (Northeastern Germany) near Berlin (Zeissler, 1962). This form, tentatively described as *P. (Cymatocyclas) casertanum plicatum* by Zeissler (1971) is characterized by a marked appendicula parallel to the growth striation, at the level of the umbo. In 1993, live specimens of *P. casertanum plicatum* were collected in the Rhine-Meuse Delta, The Netherlands (Wallbrink, 1995). In 1989, individuals which similar conchological features were found in the Saône River (Mouthon & Tair - Abbaci, 2012). A molecular genetic approach used to clarify the taxonomic position of these specimens revealed that the French individuals belonged to the North American species *Euglesa compressa* Prime, 1852 (Mouthon & Forcellini, 2017). Following the publication by Van Haaren (2015) of several photos of *E. casertana f. plicata* recorded in the Rhine-Meuse delta, we suspected that Dutch specimens also belonged to *E. compressa*. In this paper, we compare French, Dutch and North American specimens using a ribosomal DNA marker and discuss the taxonomic and biogeographic implications of this comparison.

**Material and methods**

Six individuals of *E. casertana f. plicata* were collected in 2017 in The Netherlands by one of the authors (T. v. H.), four in a waterway along Papeweg, Oud-Beijerland (51°.8166N 4°.4399E) and two in Wold Aa at Oosterboer (52°.7030N 6°.2239E). Here, we adopt the classification of Sphaerinae proposed by Lee & Ó Foighil (2003), in which *Cyclocalyx* Dall, 1903, is replaced by *Euglesa* Jenyns, 1832, according to the principle of priority (Falkner et al., 2002; Gargominy et al., 2011).
Molecular analysis

The first internal transcribed spacer (ITS-1) of ribosomal RNA, a relevant marker for species level identification (Freire et al., 2010) widely used in phylogenetic studies on Sphaeriidae (Lee & Ó Foighil, 2003; Schultheiß et al., 2008; Stunžėnas et al., 2011; Mouthon & Forcellini, 2017; Bespalaya et al., 2017) was sequenced in order to identify some Dutch specimens. For details about RNA extraction and the PCR process see Mouthon & Forcellini (2017). Both strands were sequenced by Biofidal using the Sanger method (Sanger et al., 1977). ITS-1 fragments alignment between Dutch specimens and American (Accession number: AY093518) and French (Accession numbers: KY202908, KY202910, KY202911 and KY202912) was done using Prank (Löytynoja & Goldman, 2005).

Results

Taxonomic implications. – The analysis of ITS-1 sequences (comprising 544 base pair fragments) showed no differences between American and French specimens of *E. compressa* and Dutch individuals that were originally identified as *E. casertana f. plicata*. This confirmed the presence of the North-American pea-clam *E. compressa* in the Dutch river basins (Fig. 1). The haplotypes of the French and Dutch individuals form a clade without any differences in the pairwise distances, suggesting that these populations of *E. compressa* are the result of a single introduction.

According to Van Haaren (2015), recent, empty shells of German ‘*E. casertana f. plicata*’ in Naturalis Biodiversity Center, Leiden, have similar conchological characteristics (shape, surface sculpture, hinge) as the French and Dutch *E. compressa*. Therefore, also these German specimens probably belong to this American species. Apart from this, *Euglesa casertana f. plicata*, as introduced by Zeissler (1971), is not valid according to Article 15.2 of the 1999 Zoological Code.

Biogeographic implications. – Research by T. v. H. in various collections showed that the invasive species *E. compressa* occurs in at least four European countries, viz. Germany, France, The Netherlands and Poland (Fig. 2).
The first record of *E. compressa* in Germany, collected April 3rd, 1940, by A. Tetens in the "Mühlentrieb" at Ziltendorf (Fig. 3), as *E. casertana f. plicata*, forms the first evidence of the European occurrence of this species. This brook still exists in this place, it crosses the Oder-Spree canal east of Ziltendorf and flows into the Pottak river, a tributary of the Oder. Between 1940 and 1980s, the bivalve was observed only in Northeastern Germany: in the Elbe near Hamburg (1961), in the rivers Havel, Spree, Dahme and Oder, in Tegeler See, Stientitzsee (1977) and Briesensee (1982) and in sediments of a moat at Köpenicker Castle near Berlin (Zeissler, 1962; Wallbrink, 1995). More recently, populations were reported in the Nidda River that flows into the Main before its confluence with the Rhine (Nesemann, 2016).

In France *E. compressa* was discovered for the first time in the Saône at Ouroux, September 26, 1989. Later on the species has also been found in the Rhône, Seine and Loire catchments, in various artificial canals (Marne - Rhine, Aisne - Marne), in several Rhine tributaries, the Meurthe, the Moselle and the Ill (Mouthon & Taïr - Abbaci, 2012; Mouthon et al., 2017), and in the Rhine itself, downstream from Strasbourg (van Haaren, unpublished data).

In The Netherlands, the first collection of live *E. compressa* was in the Rhine-Meuse delta (in the Biesbosch area), October 22, 1993, by Wallbrink (1995). However, Wallbrink (1995) already found empty shells along the river Lek at Lopikerkapel in 1990, indicating that the species arrived earlier. *Euglesa compressa* is very common in the Dutch fluviatile district, especially the Rhine-Meuse delta and adjacent areas. It is most often found in larger waterbodies (width > 6m) with lentic flows such as lowland rivers, large rivers (e.g. Waal, Lek, Vecht, Nieuwe Merwede, IJssel, Neder-Rijn, Kromme Rijn, Hollandse IJssel, Oude Maas, Maas, Haringvliet), large lakes (e.g. Ketelmeer, Vossemeer), sandpits and canals (e.g. Twentekanaal, Zuiderkanaal, Steenbergse Vliet). It is absent in small waterbodies such as ditches.

Samples from the Eijsder Beemden (2017), along the river Meuse at the Dutch-Belgium border (courtesy Rose Sablon, RBIN) contained several specimens of *E. compressa*. Because these samples were taken on the Dutch side, there is no official record in Belgium. However, the species is likely present in Belgium, where pea clams are little studied (R. Sablon, 2017, personal communication).

In Poland, following records from the Oder in Germany (Wallbrink, 1995), some recent samples from that river (2017, courtesy University of Szczecin) were checked for the presence of *E. compressa*. The species occurred in 2 out of the 21 samples studied, near Slubice and in the Miedzyodrze area. It is probably more widespread but may be confused with *Euglesa supina* (Schmidt, 1851).

**Discussion**

The reconstruction of the various stages of European
Colonization by *E. compressa*, suggests that it was probably introduced into Germany via the Elbe estuary and the Hamburg harbour. After its introduction in Germany, before 1940, the range of *E. compressa* remained restricted to the catchment of the Elbe and Oder in Northern Germany. In this area, researchers considered it as local form of *Euglesa casertana* (Wallbrink, 1995) or confused it with the form *ponderosa* (see Table 9, Fig. 8 in Zettler & Glöer, 2006).

Invasion processes can continue over long periods (Crooks, 2005). However, the arrival of *E. compressa* in France and in The Netherlands, seemingly about 50 years after its introduction into Germany, together with the recent reports from the river Nidda in western Germany (Nesemann, 2016) and from the Polish part of the Oder in 2017, suggest that French and Dutch specimens could come from a second, more recent introduction. The genetic analyses also showed that the French and Dutch *E. compressa* form a single clade and probably result from a same introduction (probably via the Rhine-Meuse delta). Shipping activities are considered the principal vector in the introduction of numerous species during the 20th century (Mackie, 1999; Grigorovich et al., 2003; Ricciardi, 2001; Holec et al., 2004; Duggan et al., 2005; Drake & Lodge, 2007). It is likely that this also enabled the arrival of *E. compressa* in Europe. In addition, the connection of large rivers by artificial canals may also have favoured the species spreading into The Netherlands and in France (Bij de Vaate et al., 2002). Unfortunately, pea clams are too little studied to allow a more detailed understanding of *E. compressa* colonization in Western Europe.

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**References**


