



The colonisation of the Tyrrhenian Islands by *Hydraena* water beetles, with *Hydraena reflexa* Rey, 1884 reinstated as a valid species endemic to Corsica and Sardinia (Coleoptera, Hydraenidae)

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Abstract

The biotas of old islands formed from continental terranes usually have a more complex biogeographical history than those of young oceanic islands, including taxa which have originated by vicariance and/or colonisation, over a variety of timescales. The Tyrrhenian Islands of Corsica, Sardinia and the Tuscan Archipelago in the Mediterranean have a complex geological history, shaped by interactions between the African and Eurasian plates since the Mesozoic. Our understanding of the historical biogeography of Tyrrhenian endemics remains limited for many groups, including freshwater invertebrates. Here we use a time-calibrated phylogeny, derived from mitochondrial and nuclear DNA sequence data, to explore the evolutionary history of Tyrrhenian endemic *Hydraena* water beetles, an ecologically important group in the islands' streams. Whilst no endemic *Hydraena* appear to date from the initial separation of Corsica-Sardinia from the European mainland in the Oligocene, we show that Tyrrhenian species stem from five colonisation events, occurring at different intervals in the last ca. 15 Ma, at least two endemic lineages apparently arising through isolation at the end of the Messinian Salinity Crisis. *Hydraena reflexa* Rey, 1884, long considered a geographical form or subspecies of the widespread *H. pygmaea* Waterhouse, 1833, is reinstated as a valid species, endemic to Corsica and Sardinia. *H. reflexa* can be distinguished from *H. pygmaea* on external and aedeagal characters, documented here in detail. Specimens of '*H. reflexa*' from southern continental Italy are shown to differ from those on Corsica and Sardinia, having identical male genitalia to *H. pygmaea* from elsewhere in its range. Genetically, this Calabrian form also clusters with *H. pygmaea*, and may have arisen through past introgression between a *reflexa*-like ancestor and *H. pygmaea* following the connection of the Calabrian block with the nascent Apennines in the Pliocene. The degree of genetic divergence seen between *H. pygmaea* and *H. reflexa* suggests that they diverged approximately 5.5 Ma in the Miocene, following the isolation of Corsico-Sardinian and mainland populations at the end of the Messinian.

Keywords Aquatic Coleoptera · Biogeography · Phylogeny · Hydraenidae · Island endemic · West Mediterranean

Introduction

Islands are natural laboratories for ecology and evolution, which have long fascinated naturalists; their study disproportionately contributing to ideas in biology, considering their size and scale

Ignacio Ribera passed away in 2020, before this work was completed.

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(e.g. Darlington, 1943; Lack, 1947; MacArthur & Wilson, 1967; Russell & Kueffer, 2019; Wallace, 1880; Whittaker et al., 2017). True oceanic islands, particularly hotspot archipelagos, have featured heavily in ecological and evolutionary research, investigating colonisation dynamics, patterns of endemism and adaptive radiations (e.g. Borregaard et al., 2016, 2017; Heaney et al., 2013; Whittaker et al., 2017). The terrestrial and freshwater biota of such islands is overwhelmingly composed of lineages which have colonised via trans-oceanic dispersal, something which acts as a filter and partly explains the often highly disharmonious make-up of their ecological assemblages (Carlquist, 1965; Gillespie & Roderick, 2002; König et al., 2020). In marked contrast, many of today's islands originated through a process of fragmentation of, or interaction between, continental terranes. Consequently, such islands often have a complex geological history of repeated periods of isolation

from, and connection to, other land masses, events which shape the biota of such islands in a multitude of ways (Ali, 2017).

A number of the islands in the Mediterranean Basin owe their origins to such processes, including those in the Tyrrhenian Sea west of Italy. The two largest Tyrrhenian Islands, Corsica and Sardinia, are best considered microcontinents and constitute fragments of the European continent, rifted from the southeastern margin of present-day Iberia. This process was initiated during the Oligocene due to the development of the Liguro-Provençal basin (Dercourt et al., 1986; Rosenbaum et al., 2002a; Schettino & Turco, 2006; Rossetti et al., 2015; Arragoni et al., 2016; Andreucci et al., 2017; Longhitano et al., 2017; Telesca et al., 2020), ultimately driven by interactions between the colliding Eurasian and African plates. By the mid-Miocene, some 14 Ma, Corsica and Sardinia had achieved something like their current north–south alignment, through counterclockwise rotation from their original position (Alvarez, 1972; Maffione et al., 2008; Speranza et al., 2002). During their history, Corsica and Sardinia have been connected to each other, and mainland Europe on a number of occasions. Some connection to parts of the southern edge of Palaeo-Europe may have been retained during the counterclockwise rotation of these islands, between northern parts of Corsica and the developing Maritime Alps and Ligurian Apennines (Meulenkamp & Sissingh, 2003). More dramatically, extensive links occurred during the Messinian Salinity Crisis, some 5.96 to 5.33 Ma (Cornacchia et al., 2021; Roveri et al., 2014), when these islands were widely connected to adjacent parts of southern France and the nascent Apennines. More recently, sea level fluctuations in the Pleistocene have repeatedly connected Sardinia to Corsica and the latter to mainland Italy, via the islands of the Tuscan Archipelago. These islands, including Elba, Montecristo and Pianosa owe their origin to a complex mix of geological processes, including volcanism, associated with the interaction between Corsica-Sardinia and the Apennines. Some have been connected to other land masses during periods of lower Pleistocene sea level, others remained islands (Bossio et al., 2000; Dapporto et al., 2006). The complex geology and patterns of isolation/connection between the Tyrrhenian Islands is reflected in their biota, typified by high endemism and interrelationships with species in various parts of the western Mediterranean (Caccone et al., 1994; Oliverio et al., 2000; Marra, 2004; Grill et al., 2007; Fattorini, 2009; Fattorini et al., 2016; Omodeo & Rota, 2008). Some lineages on these islands, including subterranean isopods (Ketmaier et al., 2003), subterranean beetles (Caccone & Sbordoni, 2001; Faille et al., 2018; Ribera et al., 2010) and stoneflies (Fochetti et al., 2009) appear to date from the initial split between Corsica-Sardinia and the mainland, but many are apparently more recent in origin (see Ketmaier & Caccone,

2013). Few studies have explored the timing of colonisation of these islands using calibrated phylogenies, however, and few of any nature have considered freshwater invertebrates.

Hydraena Kugelann, 1794 is the most diverse genus of aquatic beetles on Earth, with over 900 described species, distributed on all continents except Antarctica (Trizzino et al., 2013a). Named species represent an unknown fraction of the actual diversity of this genus, however; new species still being described in large numbers in recent years from tropical regions (e.g. Perkins, 2011a, b, 2014, 2022), but also from well-worked areas including Europe, albeit in smaller numbers (e.g. Bilton, 2013; Jäch & Diaz, 2012, 2016, 2017). Most species of the genus have relatively small geographical ranges, many being microendemics, restricted to single drainages or mountain ranges (e.g. Diaz Pazos & Bilton, 1995; Valladares et al., 2022). Despite its wide distribution and high endemism, and the existence of a sound phylogenetic framework for the genus (Ribera et al., 2011; Trizzino et al., 2013b) there have been very few attempts to date to utilise *Hydraena* in historical biogeographic studies. The Tyrrhenian Islands support nine species of *Hydraena*, all but one of which are considered endemic. Three members of the “*Haenydra*” lineage are known from the area (Audisio et al., 2009; Trizzino et al., 2013b), *H. evanescens* Rey, 1884, endemic to Corsica and *H. tyrrhena* Binaghi, 1961 and *H. rosannae* Audisio et al. 2009 endemic to, but allopatric in, Sardinia. Three species of the *Hydraena holdhausi* group Janssens, 1965 (Berthélemy et al., 1991) are also single island endemics: *H. aethaliensis* Breit, 1917 from Elba, *H. sardoa* Binaghi, 1961 from Sardinia and *H. subacuminata* Rey, 1884 from Corsica. In addition *H. vodozi* Sainte-Claire Deville, 1908, a species of the *H. rufipes* group, is endemic to Corsica, *H. subsequens* Rey, 1886, a species of the *H. nigrita* group is endemic to Corsica, Sardinia and parts of the Tuscan Archipelago (Elba, Capraia and Montecristo) and the widespread western Palaearctic member of the *H. minutissima* group, *H. pygmaea* Waterhouse, 1833 is represented on Corsica and Sardinia by a subspecies, *H. pygmaea reflexa* Rey, 1884 (Orchymont, 1930), which has also been recorded from Calabria in peninsular Italy (Binaghi, 1958; Pirinisu, 1981).

Here, using a time-calibrated phylogeny based on a combination of mitochondrial and nuclear DNA sequence data, we reconstruct the evolutionary and biogeographic history of the Tyrrhenian *Hydraena* fauna, revealing various timings of colonisation of these islands. Detailed re-examination of historical specimens and the degree of genetic divergence observed between *H. pygmaea* s.s. tr. throughout its range and *H. pygmaea reflexa*, leads us to reinstate *H. reflexa* as a valid species, apparently endemic to the Tyrrhenian islands of Corsica and Sardinia. On the basis of both genetics and morphology, we show that ‘*H. reflexa*’ from southern Italy differ from populations on the Tyrrhenian islands, and

suggest that this form may have arisen through introgression between *reflexa*-like animals and *pygmaea* following the connection of the Calabrian block to the nascent Apennines in the Pliocene.

Materials and methods

DNA extraction and sequencing

Specimens were killed and preserved in absolute ethanol in the field. DNA was extracted with a standard phenol–chloroform extraction or using the Qiagen DNeasy Tissue Kit (Hildesheim, Germany) following the manufacturer's instructions. In total, five specimens of *Hydraena pygmaea* s. lat. from Austria, Bulgaria, Italy, Spain and Corsica were sequenced for the same gene fragments as in Trizzino et al. (2013a): the mitochondrial cytochrome c oxidase subunit I gene (two sequence fragments, the 5' end/barcode fragment, Hebert et al., 2003 plus the 3' end), a mitochondrial fragment that amplified the 3' end of the ribosomal *rrnL* gene plus the Leucine transfer-RNA plus the 5' end of the NADH dehydrogenase subunit I gene, and two nuclear fragments corresponding with the internal fragments of the small and large ribosomal units (18S and 28S respectively). Sequences were assembled and edited with Geneious v10.2.6 (Kearse et al., 2012) and new sequences used were deposited in the sequence database GenBank (Benson et al., 2013), with accession numbers OR533284-OR533287, OR537346 and OR543921.

Phylogenetic inference and divergence time estimation

Sequences of the selected genes from species within *Hydraena* s.str. were retrieved from GenBank, together with those for three species of the subgenus *Hydraenopsis* Janssens, 1972, used as outgroups. In terms of Tyrrhenian *Hydraena*, all taxa except *H. vodozi* were represented in our dataset; this apparently rare species of the Corsican mountains was never sampled, despite repeated attempts by DTB and IR. GenBank sequences were pooled together with the newly sequenced *H. pygmaea* and *H. reflexa* and aligned using the G-INS-I algorithm in MAFFT v7.450 (Katoh & Standley, 2013). A concatenated alignment was used to estimate the best partition scheme and evolutionary models in IQTree v2.1.3 (Minh et al., 2020). Then, a Bayesian inference analysis was run in BEAST v1.10.4 (Suchard et al., 2018) with the best-fit partition scheme and models and a lognormal relaxed clock per partition. This analysis was calibrated as follows, partly based on Trizzino et al. (2013a): i) 2% rate of pairwise mtDNA divergence per Ma as in the related family Leiodidae (normal distribution; mean = 0.010;

SD = 0.001); ii) the separation between the Peloponnese and mainland Greece dated at 2.5 Ma, used for a clade formed by the sister species *H. vedrasi* Orchymont, 1931 and *H. jaechiana* (Audisio & de Biase, 1990) (normal prior, mean = 2.5; SD = 0.5; upper limit = 2.5); and iii) the mean age estimate of *Hydraena* s. str. and the subgenus *Hydraenopsis* (28 Ma for each clade). The 5' end of the cytochrome c oxidase subunit I (COI) was used to compute pairwise divergence between *H. pygmaea* specimens, including *H. pygmaea reflexa*, in Geneious v10.2.6, and to reconstruct a haplotype network using TCS v1.21 (Clement et al., 2000). PHASE (Stephens et al., 2001) as implemented within DnaSP v6 (Rozas et al., 2017), was used to estimate haplotypes for each of the specimens with 1,000 iterations, a thinning interval of 5, and a burn-in of 100. Enhanced visualization of the haplotype network was performed using tcsBU (Múrias dos Santos et al., 2016).

Morphological study

Specimens were studied using Leica MZ8 and 205C stereomicroscopes, with LED gooseneck lights diffused using a tracing paper collar and tubes derived from opaque white plastic film canisters. Habitus photographs were taken with a Canon EOS 5D mark IV camera fitted to a Leica 205C stereomicroscope, with a 1× objective lens. Specimens were illuminated with gooseneck lights, diffused with a film canister tube.

Genitalia were mounted on glass slides in Kisser's glycerol gelatine (see Riedel, 2005) and imaged using an Olympus CX31 microscope and a Canon 500D camera. All image stacks were produced by hand, and combined using Zerene Stacker software (www.zerene.com).

Exact label data are cited for specimens. // indicates a new line in label text.

Abbreviations

CBP	Collection D.T. Bilton, Plymouth, UK
CRM	Collection Ignacio Ribera, Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Muséum national d'Histoire naturelle, Paris, France
MSNG	Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy
NHMW	Naturhistorisches Museum Wien, Wien, Austria
BL	Body length (front of labrum to elytral apices)
EL	Elytral length (outer angle of shoulder to apex)
EW	Elytral width at widest point
Hw.	Handwriting (labels)

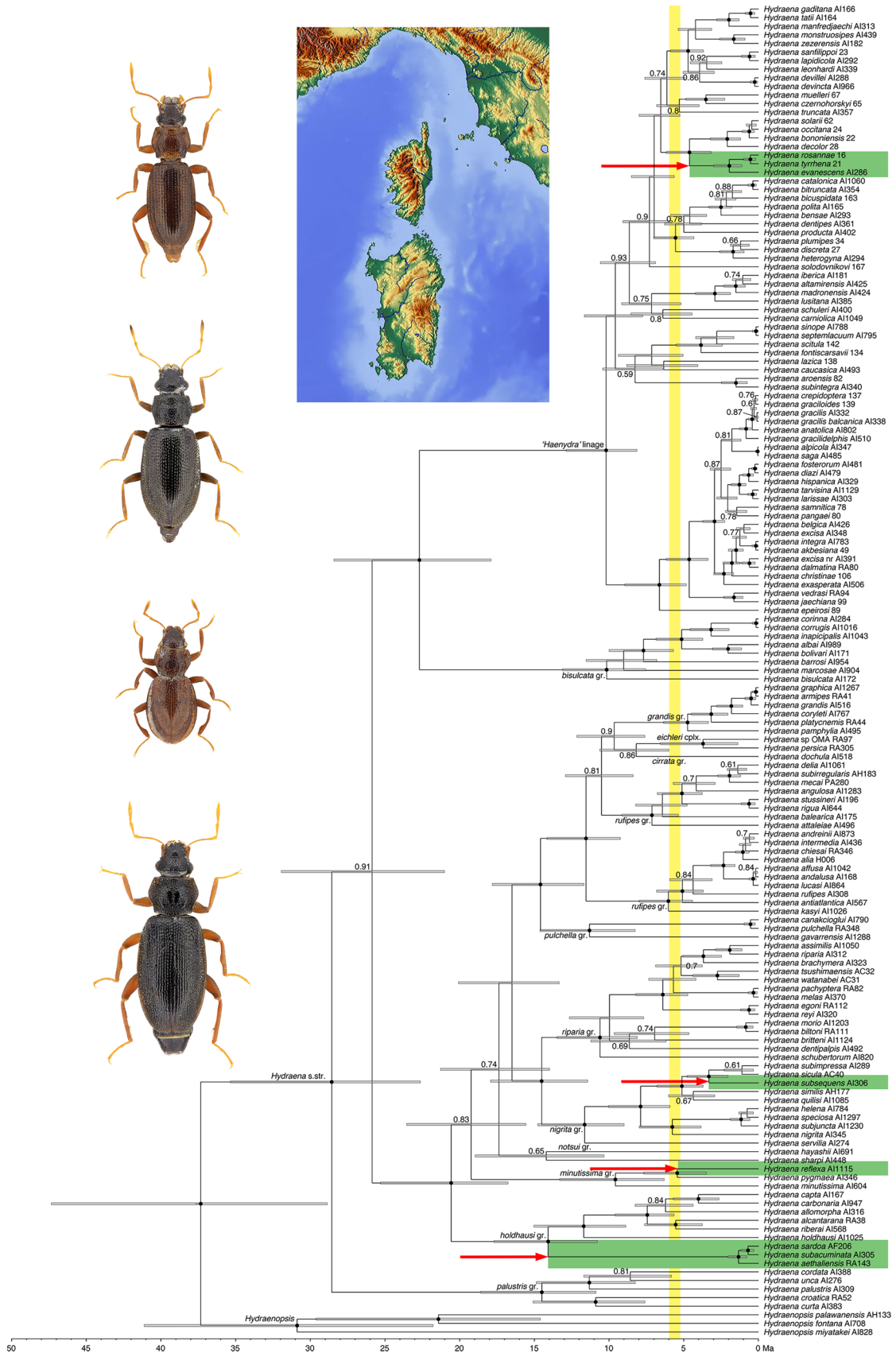


Fig. 1 Calibrated phylogenetic tree of *Hydraena* s.str. made in BEAST v1.10.4. Support values displayed at nodes as follows: black circle – support value ≥ 0.95 ; numbered nodes – support values ≥ 0.6 and < 0.95 ; no annotation – support values below 0.6. Red arrows and green shading indicate Tyrrhenian Island endemics; Yellow shading indicates approx. timing of the Messinian Salinity Crisis. Inset habitus images, top to bottom: *H. evanescens* Rey, *H. subsequens* Rey, *H. reflexa* Rey & *H. sardoa* Binaghi

Results

Phylogenetic analysis, molecular evidence and the timing of colonisation of Tyrrhenian Islands

The best partition scheme, as estimated by IQTree v.2.1.3, supports four partitions based on the sequence origin: i) the cytochrome c oxidase subunit I gene (both fragments), ii) the mitochondrial ribosomal rrrnL gene plus the leucine tRNA, iii) the NADH dehydrogenase subunit I and iv) the nuclear ribosomal gene fragments. The evolutionary model selected for the mitochondrial partitions was GTR + G + I whereas the nuclear partition relied on the K2P + G + I model. The calibrated phylogenetic analysis (Fig. 1) recovered species groups within the subgenus *Hydraena* s.str. as fully supported, but often with unresolved relationships between them. The position of Tyrrhenian island endemic *Hydraena* is indicated in Fig. 1 with red arrows and green shading. No Tyrrhenian *Hydraena* lineages are apparently old enough to date back to the separation of Corsica-Sardinia from the European continent in the Oligocene. As can be seen from Fig. 1, the clade of endemic “*Haenydra*” (*H. evanescens*, *H. rosannae* & *H. tyrrhena*) diverged from their closest mainland European relatives ca. 4.66 Ma (95% confidence interval 3.16–6.16), speciation events within this lineage being more recent at 2.10 and 0.57 Ma. Endemics of the *H. holdhausi* group (*H. aethaliensis*, *H. sardoa* & *H. subacuminata*) formed a monophyletic lineage, which diverged from included relatives ca. 14.17 Ma (95% confidence interval 10.78–17.70); speciation within this clade again being relatively recent, within the last ca. 1.37 Ma. The widespread Tyrrhenian endemic *H. subsequens* diverged from its closest relatives ca. 3.37 Ma (95% confidence interval 2.05–4.76). Finally, Corsican *H. pygmaea reflexa* diverged from remaining *H. pygmaea* ca. 5.53 Ma (95% confidence interval 3.49–7.68). COI divergence between these two taxa ranged from 7.38 to 7.7%, the maximum divergence between specimens of *H. pygmaea* being 2.73%, between a *reflexa*-like animal from Calabria in southern Italy and a morphologically standard *pygmaea* specimen from Austria (Fig. 2). Based on our molecular findings, as well as a detailed re-examination of morphology (see below), we reinstate *H. reflexa* as valid species, which is redescribed below and recognise southern Italian populations as a divergent lineage of *H. pygmaea*, which may have arisen through past hybridization.

Taxonomy

Hydraena (Hydraena) reflexa Rey, 1884

Hydraena reflexa Rey, 1884: 271.

Hydraena (Grammhydraena) reflexa Rey; Kuwert, 1888: 120.

Hydraena (Hadraena) reflexa Rey; Zaitzev, 1908: 352.

Hydraena pygmaea reflexa Rey; Orchymont, 1930: 37.

Hydraena pygmaea reflexa Rey; Ieniştea, 1978: 305.

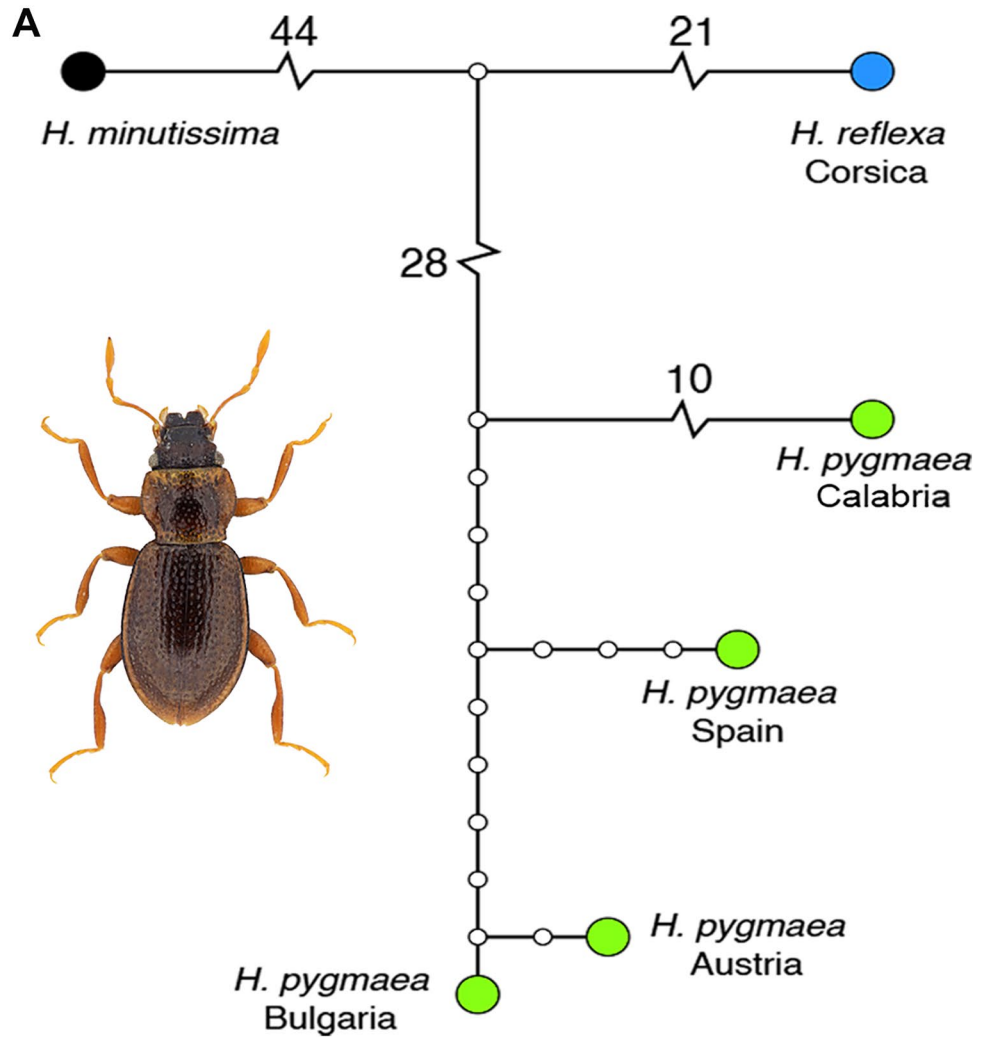
Hydraena pygmaea reflexa Rey; Pirinisu, 1981: 23 partim.

Type locality. France, Corse

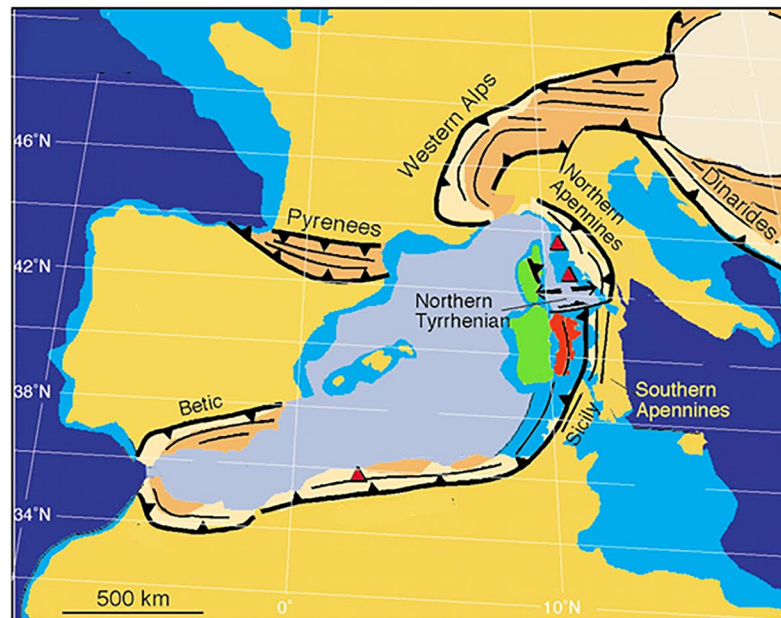
We have not seen the type material, which may be in the Rey Collection in Lyon, as it is not in Paris (A. Mantilleri pers. comm.). From Rey’s description, however, there is no doubt about the identity of this taxon, which is also the only *H. pygmaea* – group (sensu Jäch, 1988) species on Corsica. The redescription below is based on material in the Sainte-Claire Deville Collection, MNHN, specimens collected by Doderò, Binaghi and Ferro in NHMW and MNSG and a single female taken by DTB in 2006.

Material examined. Corsica: 1 ♂ (MNHN) “Monte d’Oro// Corse” “*H. reflexa*” [Hw.] “MUSEUM PARIS// 1932// COLL. STE. CL. DEVILLE” “MNHN, Paris// EC17121”; 1 ♀ (MNHN) “Monte d’Oro// Corse” “*Hydraena// reflexa* Rey” [Hw.] “MUSEUM PARIS// 1932// COLL. STE. CL. DEVILLE” “MNHN, Paris// EC17120”; 1 ♀ (MNHN) “Monte d’Oro// Corse” “MUSEUM PARIS// 1932// COLL. STE. CL. DEVILLE” “MNHN, Paris// EC17122”; 1 ♂ (MNHN) “Monte d’Oro// Corse” “MUSEUM PARIS// 1932// COLL. STE. CL. DEVILLE” “MNHN, Paris// EC17123”; 1 ♂ (MNHN) “Bocognano// Corsica Vod.” “*reflexa// Rey*” [Hw.] “MUSEUM PARIS// 1932// COLL. STE. CL. DEVILLE” “MNHN, Paris// EC17124”; 1 ♀ (MNHN) “Bocognano// Corsica Vod.” “MUSEUM PARIS// 1932// COLL. STE. CL. DEVILLE” “MNHN, Paris// EC17125”; 1 ♀ (CRM) “13/ix/2006 France Corsica// Stream 5 km N of Col de la// Vaccia on D69 N of Aullence// ca. 1,100 m D T Bilton leg.” “MNCN-AI1115”; 1 ♂ (NHMW) “Monte d’Oro// Corse” “*Hydraena// reflexa* Rey [Hw.] “*pygmaea* ssp. *reflexa// det. E. Pretner*” [Hw.] “*Hydraena// reflexa* sp. propr.// det. M. Jäch 03” [Hw.] “Collect.// Hauser”; 1 ♂ (NHMW) “Monte d’Oro// Corse” “*reflexa* Rey” [Hw.] “*pygmaea// ssp. reflexa// det. E. Pretner*” [Hw.]; 1 ♂ (NHMW) “Vizzavona// Corse// Vodoz” [Hw.] “*reflexa* Rey// ♂” [Hw.] “*pygmaea// ssp. reflexa// det. E. Pretner*” [Hw.] “*Hydraena// reflexa// det. Jäch 1986*” [Hw.]; 1 ♂ (NHMW) “Coll.//Hampe” “607” “illegible” [Hw.] “*reflexa// Rey* Kuw.” [Hw.]; 1 ♂ (MNSG) “Corsica// Serra di Scopamène// Cargiaca 539 m// 16.9.91 leg. Ger” [Hw.] “*Hydraena// (s.str.) reflexa// det. G. Ferro*” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”; 2 ♂ (MNSG)

Fig. 2 COI variation in the *Hydraena minutissima* group. **A)** Haplotype network for sequenced specimens of the group. Empty circles indicate mutational steps between haplotypes, inset male *H. pygmaea*; **B)** approximate position of land masses in the Western Mediterranean during the Miocene, ca. 6 Ma. (modified after Rosenbaum et al. (2002b)). Corsica-Sardinia green, Calabrian block red, shelf light blue. Note that during the Messinian Salinity Crisis, much of the basin was dry



B



“F 26, Corse (2A),// Serra-di Scopamène,// Cargiaca, Amor do// Diu. 09°03E, 41°44N,// 530 m, 26.09.91, leg.// GER.” “*Hydraena*// (s.str.) *reflexa*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”; 1 ♀ (MNSG) “aureole// lucido// mancanti” [Hw.] “Corsica// Serra di Scopamène// Cargiaca 539 m// 16.9.91 leg. Ger” [Hw.] “*Hydraena*// (s.str.) *reflexa*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”. **Sardinia:** 1 ♂ (MSNG) “ARITZO// Sard.// VII – 1911// A. Dodero” “*Hydr. pygmaea*// ssp. *reflexa* Rey// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”; 1 ♂ (MSNG) “Sardegna// Nu – Talàna// 13.9.91 Ger.” [Hw.] “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”.

Redescription. Size: Males BL 1.70–1.75 mm; EL 1.05–1.10 mm; EW 0.70–0.75 mm. Females BL 1.70–1.75 mm; EL 1.05–1.10 mm; EW 0.75–0.80 mm.

Colour: Dorsum (Fig. 3A–B and 6C) predominantly reddish brown; pronotal and elytral margins paler; head slightly darker. Antennae, maxillary palpi and legs yellow to reddish brown. Venter reddish brown; pronotal hypomera and elytral epipleurs paler.

Head: Broadly triangular, broadest at hind margin of eyes; narrowing in front of clypeus; narrowest at base of labrum. Compound eyes medium, occupying approximately 1/3 of side margin of head excluding labrum. Labrum slightly transverse, deeply emarginate anteromedially, creating two rectangular lateral lobes; lobes widest at base. Anterior and lateral margins slightly thickened and upturned, with short, decumbent setae. Surface shining, without evident microreticulation, with sparse, fine punctures. Clypeus, frons and vertex shining, with sparse, medium to large punctures bearing long, fine, adpressed setae; punctures 1.5–3 puncture widths apart. Frontoclypeal suture indistinct, represented by a puncture line and change from lighter frons to slightly darker clypeus only. Frons much wider than clypeus, with distinct, rounded, slightly obtuse anterolateral angles. Lateral margins of clypeus and frons with dense, rugose micropunctation, particularly inside compound eyes. Maxillary palpi unmodified.

Pronotum: Slightly transverse, cordiform, broadest in front of middle. Sides dentate, with distinct raised lateral border; broadly rounded at broadest point, then weakly concave to hind angles and weakly convex to front angles. Hind angles weakly pointed, slightly obtuse; front angles rounded, obtuse. Front margin with broad, very shallow emargination in central half, then almost straight to front angles. Hind margin weakly bisinuate around centre. Disc shining, devoid of microreticulation; with sparse, medium to large, shallow punctures bearing fine recumbent to decumbent setae; spaced 0.15–3 puncture diameters apart. Anterolateral pronotal foveae round, deep, pit-like, opening anteriorly; posterolateral pronotal foveae smaller and shallower, again

round and pit-like. Interior of fovea rugose due to dense micropunctation.

Elytra: Very broad, slightly elongate, widest just behind middle. Sides rounded to cojointly emarginated and acuminate apex. Elytral margin minutely serrate, reflexed, from just behind shoulder to close to apex; margin broadly explanate. Elytra shining, with 5–7 irregular, non-striate rows of large, shallow punctures, bearing fine recumbent setae between suture and elytral shoulder; punctures becoming very shallow and obsolete in apical half. Elytral disc somewhat domed around suture, otherwise slightly flattened just behind shoulder in anterior half, gradually declining to apex over posterior half.

Wings: Micropterous, reduced to short flaps, with limited venation.

Venter: Mentum transverse, strongly acuminate apicomediaally; anterior margins with sparse, stout, suberect peg-like setae; surface shining, with open isodiametric to slightly transverse microreticulation and sparse, fine punctures bearing short recumbent to decumbent setae; somewhat rugose posteriorly and laterally. Submentum shining, with shallow, sparse medium punctures and open isodiametric to slightly transverse microreticulation. Gena shining centrally, rugose laterally. Prosternal intercoxal process carinate, rugulose sculptured. Pronotal hypomera broad, weakly shining, with fine, rugulose reticulation. Elytral epipleura very broad, shining; continued almost to apex; with sparse, fine punctures bearing fine setae anteriorly. Mesoventrite dull, strongly and rugulose microreticulate, with dense setose vestiture; mesoventral intercoxal process parallel sided, dull, lateral margins raised. Metaventrite rugulose punctured with dense vestiture and transverse posteromedian depression; anterior margins strongly raised behind mesocoxae. Mesoventral plaques elongate, very narrow, curvilinear; shining and slightly raised above rest of ventrite, flanking posteromedian depression. Abdominal intercoxal sclerite width at arcuate posterior margin approx. 2× that of apex of mesoventral intercoxal process. Abdominal ventrites 1–4 shining in centre, with dense hydrofuge vestiture laterally; ventrite 5 with dense vestiture and glabrous, shining patch in centre restricted to posterior half. Ventrite 6 shining, devoid of vestiture.

Legs: Relatively short. Mid and posterior tibiae strongly modified, curved, expanded characteristically towards apices (Fig. 5A–B; 6G).

Aedeagus: Elongate (Fig. 4A–B; 6F); distal lobe with gonopore-bearing flagellum long, arcuate, curved in a circular manner over apex of main piece in dorsal view; secondary lobe shorter and broader, funnel-like. Main piece straight or nearly so in dorsal view, narrowing at insertion of distal lobe and narrow apical portion curving slightly to the right in dorsal view; straight in lateral view, broadly arcuate towards the base and curved downwards. Parameres

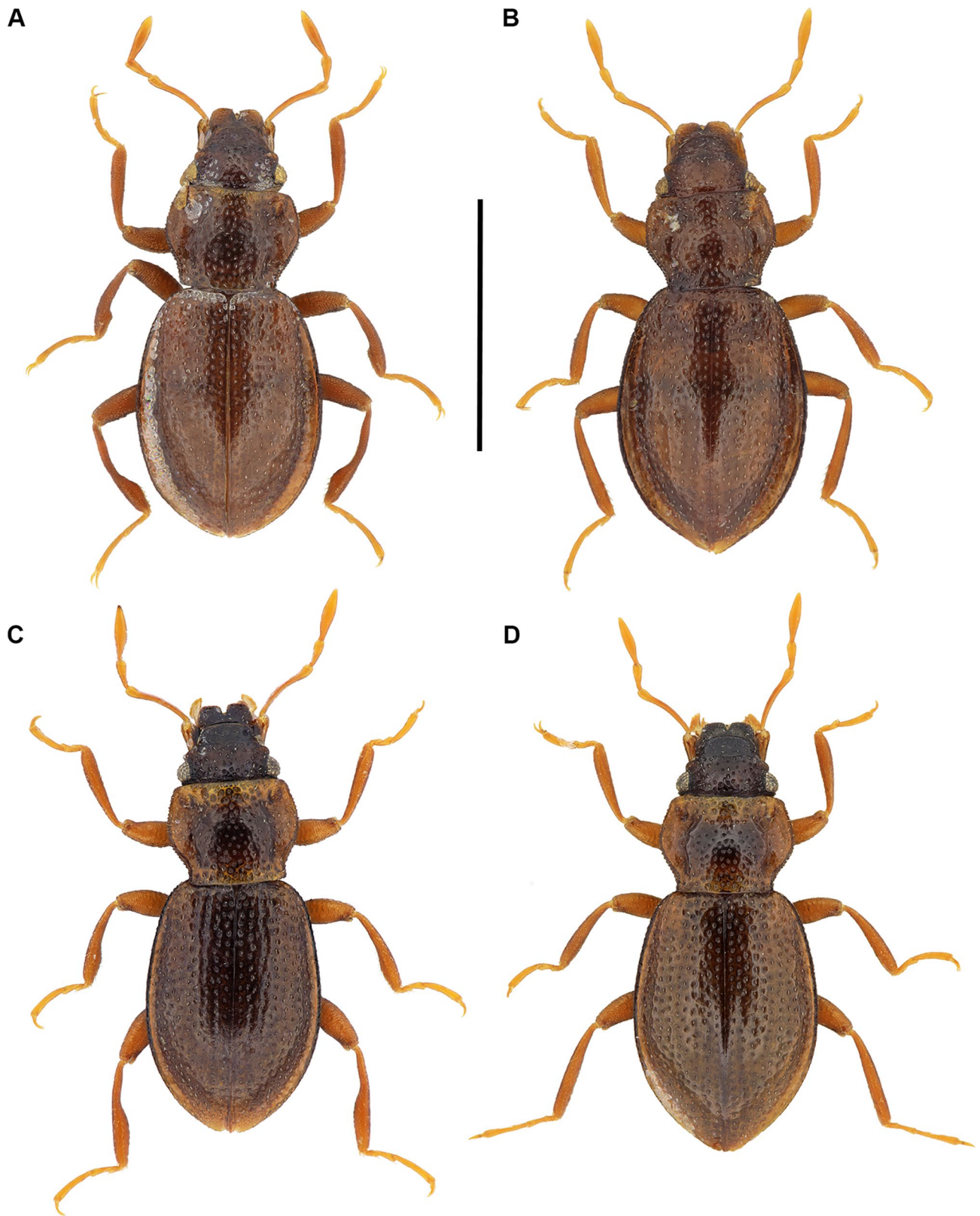


Fig. 3 *Hydraena* species habitus. **A–B** *Hydraena reflexa* Rey, Monte d’Oro, Corsica; **C–D** *Hydraena pygmaea* Waterhouse, Ruddycleave Water, South Devon, UK. **A & C** males; **B & D** females. Scale bar = 1.0 mm

elongate, surpassing mid-point of main piece; right longer than left, each with brush of long apical setae.

Female: Similar to male, but with lateral margins of elytra more strongly reflexed, and bordered internally by a gutter-like channel (Fig. 3B). Mid and hind tibiae unmodified.

Differential diagnosis. Clearly similar to *H. pygmaea*, resembling this species in overall habitus and aedeagal design. *H. reflexa* can be distinguished from all except southern Italian populations of *H. pygmaea* (Calabria and parts of Basilicata – see Fig. 6) by the much more strongly reflexed, explanate elytral margins, particularly in females (Fig. 3). It can be distinguished from all known *H. pygmaea* by the more rounded elytral margin and the elytral disc being more strongly domed around the suture, by the different leg modification in males (Figs. 5 and 6), and by subtle but consistent differences in the distal lobe of the aedeagus (Fig. 4 and 6).

Whilst Corsican and Sardinian male leg modifications do differ (compare Fig. 5A–B and Fig. 6G), greater curvature of the hind tibia (compared to *H. pygmaea*) is seen in all specimens. In all examined *H. pygmaea*, including specimens from Calabria and Basilicata, the gonopore-bearing flagellum is relatively long and always curves backwards, towards the secondary lobe in lateral view (Fig. 4C–E; 6D), whereas in *H. reflexa* this structure is shorter and somewhat adpressed against the secondary lobe towards its apex (Fig. 4A–B; 6F). In dorsal view, the curvature and arrangement of the distal lobes of the two species is also consistently different (see Figs. 4 and 6); the gonopore-bearing flagellum being shorter and curving back over the apex of the main piece in *H. reflexa*, instead orientating away from the main piece in *H. pygmaea*. The secondary lobe of the distal lobe is funnel-like in both species, but again differs

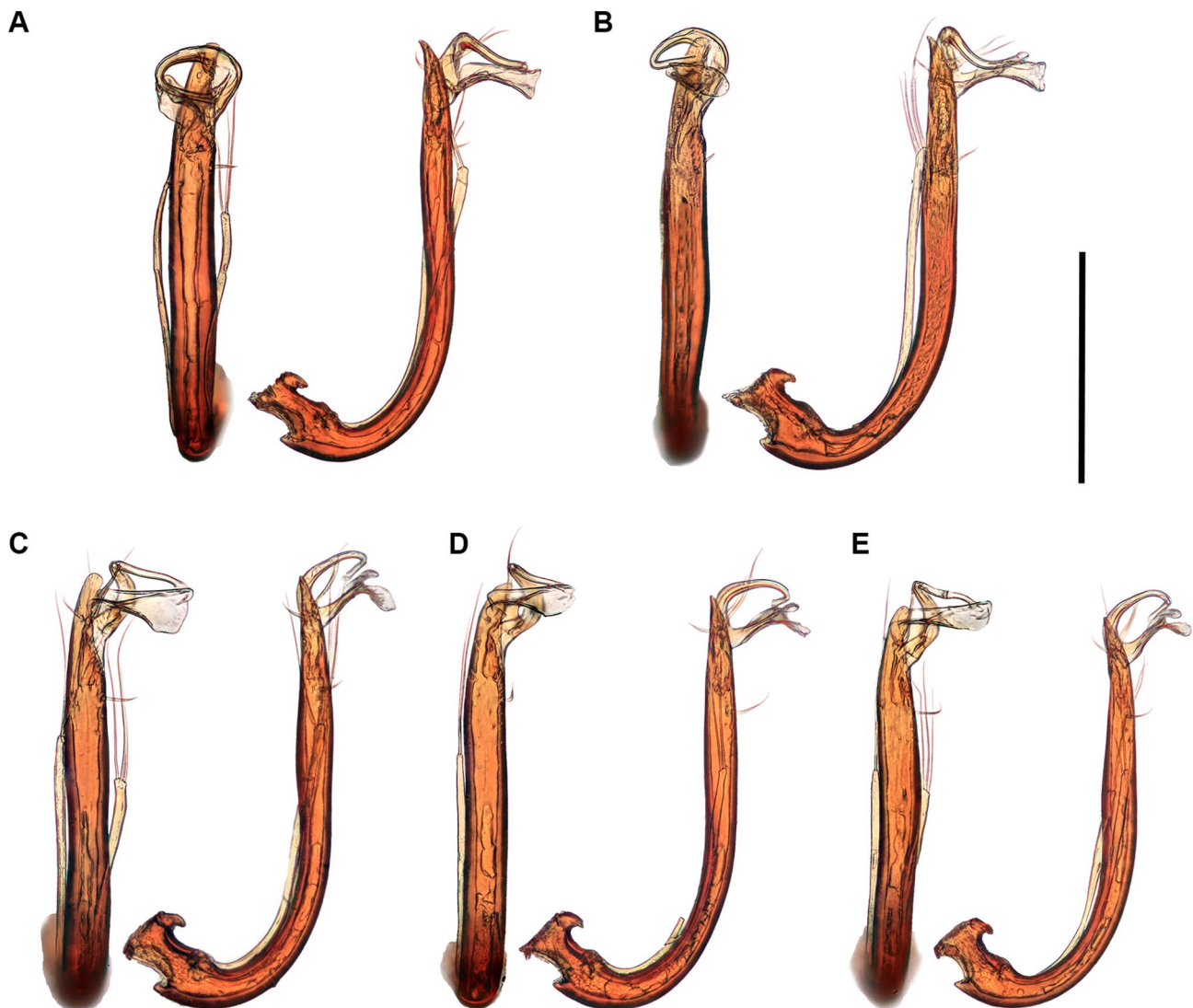


Fig. 4 *Hydraena* species aedeagi. **A–B** *Hydraena reflexa* Rey, Monte d’Oro, Corsica; **C–E** *Hydraena pygmaea* Waterhouse; **C** Rio de las Hoyas, Albacete, Spain; **D** stream above Bacevo, Rila Mts., Bulgaria; **E** Ruddycleave Water, South Devon, UK. Scale bar = 100 μ m

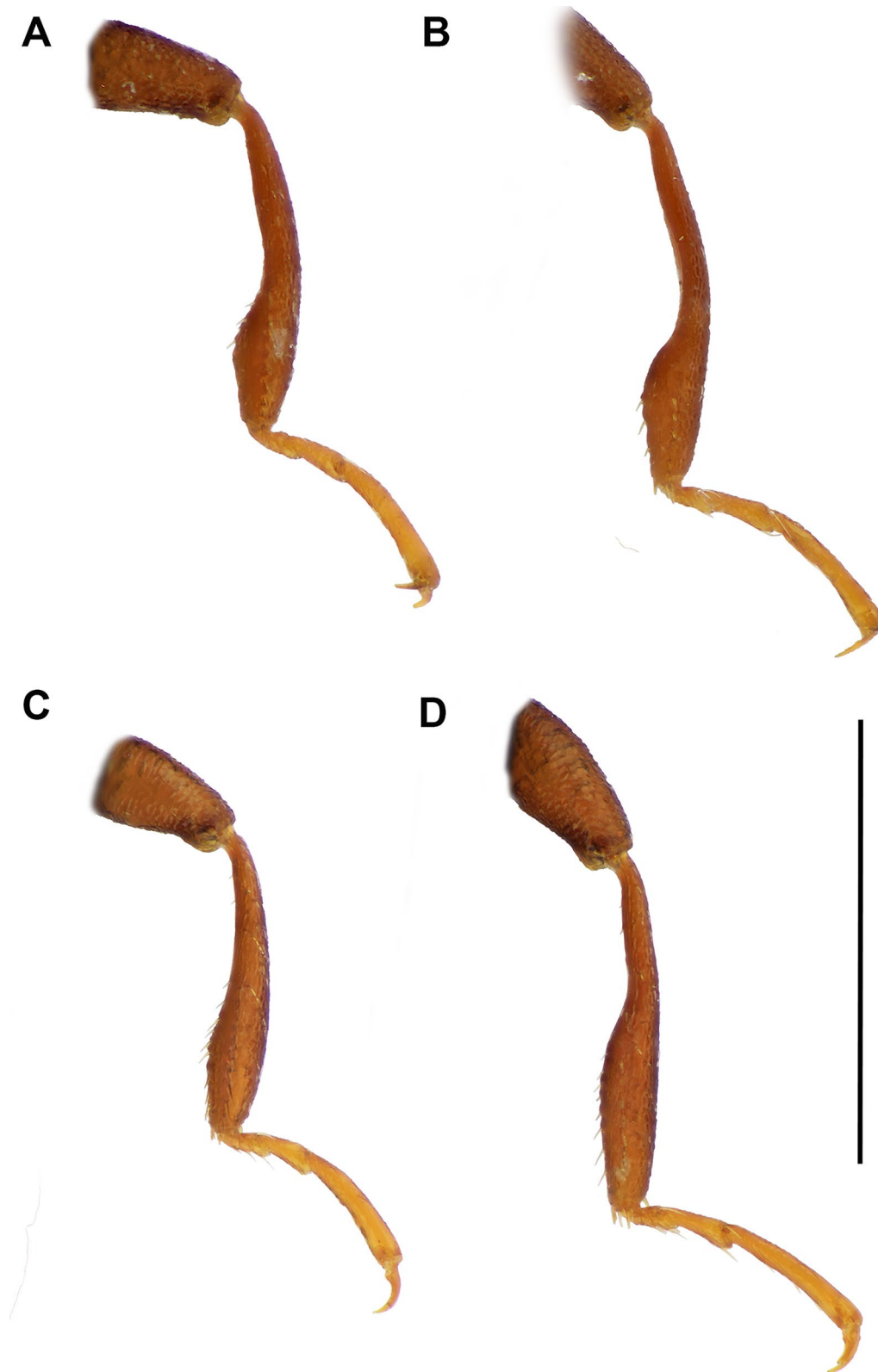


Fig. 5 *Hydraena* species, male leg modifications. **A–B** *Hydraena reflexa* Rey, Monte d’Oro, Corsica; **C–D** *Hydraena pygmaea* Waterhouse, Ruddyleave Water, South Devon, UK. **A & C** mid legs; **B & D** hind legs. Scale bar=0.50 mm

in detail; that of *H. reflexa* is narrower, typically directed more dorsally in dorsal view and less opened apically than the equivalent in *H. pygmaea* (Fig. 4). Interestingly, as can be seen in Fig. 4, the size of the aedeagi differ somewhat between specimens in both species.

Distribution and ecology. Known with certainty only from the Tyrrhenian islands of Corsica and Sardinia, where it occurs in mountain streams (Schaeffer, 1964; Audisio & De Biase, 2005). Apparently a rather scarce species, particularly on Sardinia, few individuals being locatable in collections. Records from mainland Italy (e.g. Binaghi, 1958; Pirinisu, 1981) are based on superficially similar beetles with explanate elytra, which are considered conspecific with *H. pygmaea* (see below).

Hydraena (Hydraena) pygmaea Waterhouse, 1833

Hydraena pygmaea Waterhouse, 1833: 295.

Hydraena (Hadraena) pygmaea Waterhouse; Ganglbauer, 1904: 215.

Hydraena (Hadraena) pygmaea Waterhouse; Reitter, 1909: 356.

Hydraena (s.str.) *pygmaea* Waterhouse; Orchymont, 1936: 64; Balfour-Browne, 1958: 194; Valladares et al., 2018: 189.

Hydraena Sieboldii Rosenhauer, 1847: 28.

Hydraena (Hadraena) Sieboldi [!] Rosenhauer; Rey, 1886: 110.

Hydraena (Grammhydraena) Sieboldi [!] Rosenhauer; Kuwert, 1888: 120.

Hydraena lata Kiesenwetter, 1849: 188.

Type locality. Hebden Bridge, Yorkshire, UK.

We have not been able to locate the type series, which is not in Waterhouse's material in the Natural History Museum, London (M. Barclay pers. comm.). Waterhouse based his description on specimens collected by a Samuel Gibson, whose collection was, at one time, in the Peel Museum, Manchester. Enquiries at Manchester, Liverpool and Salford Museums all failed to locate any *H. pygmaea* likely to emanate from Gibson, and this material may be lost. There is no doubt about the identity of this widespread species, however, the name having been used consistently by almost all authors since its introduction. See Valladares et al. (2018) for a thorough, modern description with figures.

Material examined. Great Britain: 3 ♂ 3 ♀ (CBP) "10/v/2009 England S Devon// Ruddy Cleave Water nr// Buckland in the Moor// D T Bilton leg."; 1 ♂ 1 ♀ (CBP) "15/x/2005 ENGLAND// S Devon River Gara @// Gara Mill above Strete// D T Bilton leg."; 1 ♀ (CBP) "D. T. Bilton// H. pygmaea// seepage near// Bewcastle 11/iv/83" [Hw.]; 1 ♂ (CBP) "D. T. Bilton// H. pygmaea// Conic Hill// Lochlmondside// 28/vi/1983" [Hw.]; 5 ♂ 5 ♀ (CBP) "4/vi/2021 Wales Black Mountains// Nant Bwch at junction with

Nant Ganol// SO232333 530 m, river moss// D T Bilton leg.". **France:** 1 ♂ (NHMW) "Guillebeau// Frankreich" "♂" "sieboldi" [Hw.]; 1 ♂, 3 ♀ (NHMW) "Fauvel// Calvados"; 2 ♂, 2 ♀ (NHMW) "Elsass" "Hydraena// sieboldi" [Hw.] "pygmaea" [Hw.] "Hydraena// pygmaea Waterh.// det. M Jäch". **Germany:** 1 ♂ (NHMW) "sieboldi// Rothenh." [Hw.] "♂" "c. Epplsh.// Steind.d." [Hw.] "107" [Hw., green label] "alleged Paralectotype// H. sieboldi Rosenhauer// vid. Jäch & Diaz 2000" [Hw., red label]; 1 ♀ (NHMW) "sieboldi// Erlangen// Rosenhauer" [Hw.] "106" [Hw., green label] "c. Epplsh.// Steind.d." "sieboldi" [Hw.]; 1 ♀ (NHMW) "Coll.// Hampe" "sieboldi// Rosh. Bav" [Hw.]; 1 ♂ (NHMW) "sieboldi Rosh.// Baden-Baden.// Sept. 79" [Hw.] "♂" "401" [Hw., green label] "c. Eppelsh.// Steind.d." "sieboldi" [Hw.]; 1 ♂, 1 ♀ (NHMW) "Oberbayern// leg. Hebauer" "St. Heinrich// 4.4.1976" "Hydr.// pygmaea" [Hw.]; 2 ♀ (NHMW) "D-BAYERN: 2.11.1996// E. Stuttgart// Weinstadt-Baach// leg. M. Jäch (D2)"; 1 ♂, 1 ♀ (NHMW) "DDR 22.5.86// Drachenschlucht// bei Eisenach// leg. Jäch [Hw.]; 1 ♂ (NHMW) "Dresden" [Hw.]; 1 ♂, 1 ♀ (NHMW) "Seis, TL// Schuster". **Austria:** 1 ♂ (NHMW) "Austria VLBG 13229// Schwarzach 410 m// 13.6.1995// Unterwassermoos// leg. C.M. Brandstetter" "H. pygmaea" [Hw.]; 1 ♂ (NHMW) "A-VLBG: Bez. Dornbirn// N Dornbirn, 3.6.2001// Haselstauder Bach, 410 m// leg. Jäch (2)"; 1 ♀ (NHMW) "A-VLBG: Bez. Bregenz// ca. 1,5 km N Hörbranz// 2.6.2002, ca. 425 m// leg. Jäch (1)"; 1 ♂ (NHMW) "A-VLBG: Bez. Bregenz// 0,7 km NNW Hohenweiler// 2.6.2001, 460 m// leg. Jäch (2)"; 1 ♂ (NHMW) "SALZBURG: Flachgau// SW Seidenfeld, 600 m// NNE Plainfeld, 27.7.1999// leg. Jäch et al. (6)"; 1 ♂, 1 ♀ (NHMW) "A-KÄRNTEN: Klagenfurt/Land// 1 km SW Stuttern, 26.8.2001// Stutterner Moos, 475 m// leg. Raunig (1)"; 4 ♂, 3 ♀ (NHMW) "Umg. Linz O. Ö// H. Priesner"; 1 ♀ (NHMW) "A- Styria, Bez. Weiz// Raubklamm ca. 5 km NW Weiz// 15°33'28"E 47°14'08"N 540 m// 28.7.2000 leg. Jäch (5)" "Hydraena// pygmaea Waterh.// det. M. Jäch"; 2 ♂ (NHMW) "Vorarlberg// Hohenweiler// Richenbach 470 m// 5.5.1993 Detritus// Wasserwehr// leg. Ing A Kapp 1680" "Hydraena// pygmaea Waterh.// det. M. Jäch"; 10 ♂, 6 ♀ (NHMW) "Vorarlberg// Hohenweiler// Richenbach 470 m// 5.5.1993 Detritus// Wasserwehr// leg. Ing A Kapp 1680" "Hydraena// pygmaea// Jäch det. 1994" [pygmaea & 4 Hw.]; 1 ♂, 1 ♀ (NHMW) "AUSTRIA Vorarlberg// Hohenweiler// Rohrach 29.4.1993// 590 m Detritus unter// wasserfall// leg. Ing A Kapp 1669" "Hydraena// pygmaea// Jäch det. 1994" [pygmaea & 4 Hw.]. **Slovenia:** 4 ♀ (NHMW) "YU – Slovenija// 20 km N Kranj// leg. Jäch 27.6.88"; 1 ♀ (NHMW) "YU – Slov. Jäch// Selščica 23.6.84// W. Želenzniki" [Hw.]; 1 ♂ (NHMW) "YU – Slov. 25.6.88// PaulitschS.// Steiner A.// Jäch" [Hw.]. **Bosnia and Herzegovina:** 1 ♂ (NHMW) "BOSNIA// Banja Stijena// 1931. VII. 2–24.// leg. Dr. J. Fodor". **North Macedonia:** 1 ♂ (NHMW) "YU – Maked. 12.8.88// nw Gergeljia// leg. Jäch (85)"; 1 ♂

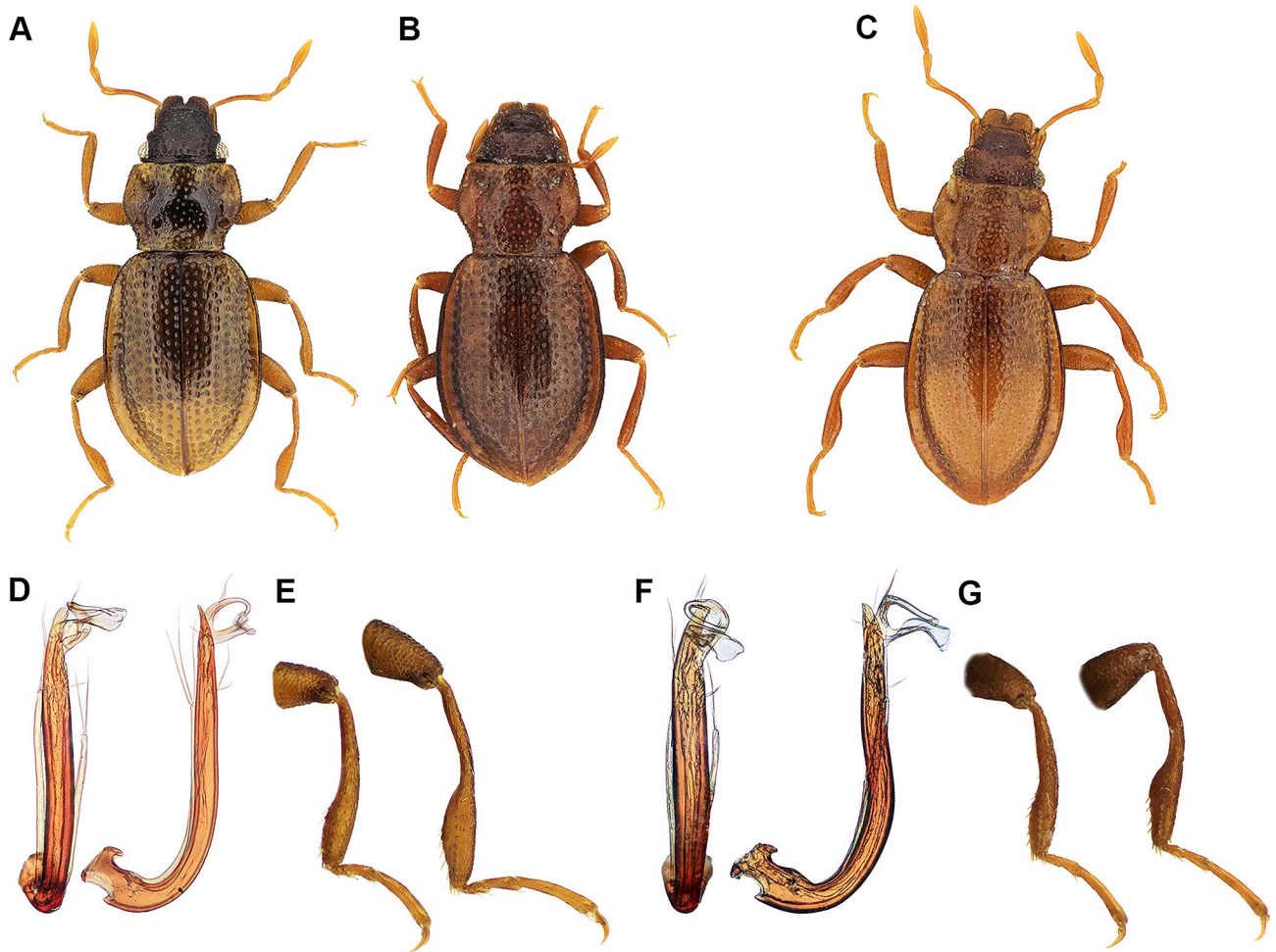


Fig. 6 *Hydraena* species, Calabria and Sardinia. A) *Hydraena pygmaea* male Calabria, Sila, Camigliatello, habitus; B) *Hydraena pygmaea* female Calabria, Sila, Camigliatello, habitus; C) *Hydraena reflexa* male Sardinia, Aritzo, habitus; D) *Hydraena pygmaea*

male Calabria, Sila, Camigliatello, aedeagus dorsal and lateral; E) *Hydraena pygmaea* male Calabria, Sila, Camigliatello, mid and hind legs; F) *Hydraena reflexa* male Sardinia, Aritzo, aedeagus dorsal and lateral; G) *Hydraena reflexa* male Sardinia, Talàna, mid and hind legs

(NHMW) “YU – Maked. 27.7.88// Pelister bei// Bitola: Jäch (11)”. **Spain:** 1 ♂ (NHMW) “ESPANA: Granada, 24.10.1998// Sierra Nevada, 1100 m// Rio Maitena// leg. M. Jäch (19)”; 1 ♀ (CBP) “17/vi/2006 Spain Albacete// Rio de las Hoyas @ Puerto// de Madera D.T. Bilton leg.”; 1 ♂ 2 ♀ (CBP) “27/vii/2012 Spain Albacete// Rio de las Hoyas @ Cortige// de Torta D T Bilton leg.”; 1 ♀ (CBP) “10/vi/2013 Spain Guip// PN de Aralar – stream// 1 km SE of Osinbeltz// D T Bilton leg.”; 1 ♀ (CBP) “4/ix/2013 Spain Albacete// Rio de las Hoyas// en el Cortijo de Tortas// D T Bilton leg.”. **Slovakia:** 1 ♂ (NHMW) “CSFR – Slowakei// Muran (1)// 17.10.1991 Jäch” “*Hydraena// pygmaea* Waterh.// det. M. Jäch”; 1 ♂ (CBP) “8/vi/2009 Slovakia// River above Jablonové// 362 m D T Bilton leg.”. **Greece:** 1 ♂ (NHMW) “GR mt. Ossa// Stomion 19.6.86// leg. H. Hebauer”; 4 ♂, 1 ♀ (NHMW) “GR-Rodopi 8.8.88// Dipotama// leg. Jäch (75)” [same card]; 1 ♂ (NHMW) “GR – Thassos 1991// Potamias (1)// leg. M. Jäch 9.IX.” “*Hydraena// pygmaea* Waterh.// det. M. Jäch”; 1 ♂

(NHMW) “GR – Euböa (6)// Steni-Stroponas// 650 m 30.IX.// leg. Jäch 1992”; 1 ♂ (NHMW) “GR: Ioannina, 21.9.1999// unterh. Metsovo, ca. 1000 m// 39.78886N 21.21666E// leg. Hess & Heckes (1)” “HYDRAENA// *pygmaea* WAT.// A. Skale, 2003”; 1 ♂ (NHMW) “GR – Ioannina: 29.4.2000// NE Ioannina, 3 km NNE Grevenniti// 39° 49.7'N 21° 00.8E// ca. 950 m, leg. Komarek// Schillhammer, Schönmann (23)” “HYDRAENA// *pygmaea* WAT.// A. Skale, 2004”; 1 ♂ (CBP) “3/viii/2012 GR Peloponnese// Taygetos Mts. Loga Bk. @// 800 m above Anoghia// D T Bilton leg.”. **Bulgaria:** 3 ♂ 2 ♀ (CBP) “5/vii/2005 Bulgaria// Rila Mts. Stream @ 1,500 m// Above Bacevo// D. T. Bilton leg.”; 2 ♂ (CBP) “9/vii/2005 Bulgaria// Rhodope Mts. Stream @ 800 m// Above Filipovo// D.T.Bilton leg.”. **Turkey:** 5 ♂, 2 ♀ (NHMW) “TR – THRACIA 28.7.// Istranca (30)// leg. Jäch 1998”; 1 ♂, 1 ♀ (NHMW) “TR – ORDU 28.5.// Gököy (18)// leg. Jäch 1989”; 2 ♀ (NHMW) “TR – ERZINCAN 10.6.// sö Refahiye// leg. Jäch 89 (77)”; 1 ♂ (NHMW) “TR:ARTVIN// ca/ 25 km//

NNW Borçka” “Kargöl// leg. A. Kasapoğlu// 16.IX.2000” “*Hydraena*// *pygmaea* WAT.// det. Jäch 2001”; 3 ♂ (NHMW) “TR – ARTVIN 5.6.// Savsat (54)// leg Jäch 1989”; 1 ♂, 1 ♀ (NHMW) “TR – ARTVIN 98// W. Borcka (45)// leg. Jäch 4.6.”; 1 ♂ (NHMW) “TURKEY: Artvin// Karagöl// 1470 m// leg. N. Ertorum” “HYDRAENA// *pygmaea* WAT.// A. Skale, 2011”; 1 ♂ (NHMW) “TR – ERZURUM 9.6.// Tortum (76) leg. Jäch 1989”; 1 ♀ (NHMW) “TR – ERZURUM 31.5.// Ovitgagi P. 2000 m// leg. Jäch 89 (35)”. **Armenia:** 2 ♀ (NHMW) “ARMENIA: E Yerevan// 40° 08.39’N 44° 49.12’E// nr. Gekhard, 5.5.2001// ca. 1600 m, leg. Shaverdo// & Schillhammer (16)” “HYDRAENA// *pygmaea* W.// A. Skale, 2009”; 1 ♂ (NHMW) “ARMENIA: N Yerevan// 40° 30.04’N 44° 36.86’E// nr. Arzakan, 5.5.2001// ca. 1900 m, leg. Shaverdo// & Schillhammer (23)” “HYDRAENA// *pygmaea* W.// A. Skale, 2009”; 1 ♀ (NHMW) “ARMENIA: N Yerevan// 40° 37.35’N 44° 28.02’E// ca. 30 km NW Hrazdan// 19.5.2001, ca. 2050 m// Shaverdo & Schillhammer (54)” “HYDRAENA// *pygmaea* W.// A. Skale, 2009”. **Italy, typical *pygmaea*:** 1 ♂ (MSNG) “Cividale UD-// T.Patok 300 m-// leg. Ferro IX 75.” “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”; 1 ♀ (MSNG) “f#” “Cividale UD-// T.Patok 300 m-// leg. Ferro IX 75.” “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”; 1 ♀ (MSNG) UD. Tramonti// di Sotto. maro [?]/ loc. Campone// 23.10.99. Ferro” [Hw.] “Tor. Chiarzò” [Hw.] “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”; 2 ♂ (MSNG) “POFFABRO PN.// T-Colvera// leg. Ferro” “m.448// 15 IV 77// leg. Ferro” “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”; 1 ♂, 1 ♀ (MNSG) Pinzano// PN. 24.4.89// lg Ferro” [Hw.] “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)” on same pin; 1 ♀ “[illegible] 82// COLVERE, M. Suf// Pre ALPI CARNICHE// leg. Seriani M.” [Hw. Except ALPI CARNICHE// leg. Seriani M.] “*pygmaea*” [Hw.] “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”; 2 ♂ (MNSG) “cascata// V-Veneto TV-// Leg. Ferro IV.76” “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)” on same pin; 1 ♀ (MSNG) “Bassano// Torrente// 27.9.79 Ferro” [Hw.] “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”; 1 ♂, 1 ♀ (MNSG) “Cascata Seravalle// V-Veneto TV.// 5.VI.75// Ferro” [Hw.] “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)” on same card; 3 ♂ (MSNG) “Cascata Seravalle// V. Veneto TV.// 5.VI.75// Ferro” [Hw.] “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)” on same pin; 2 ♂ (MNSG) “Feltre BL// Val. Canzal [?]/ T. ce ordine [?]/2.8.90 Ferro” [Hw.] “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono

2013)” on same pin; 1 ♀ (MSNG) “Toscana PI// Vallombrosa// T. Paradisino// m 1100. 20.8.02” [Hw.] “Protomagno// Papi R. leg.” [Hw.] “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”; 1 ♂ (MSNG) “Rossina// T. Sacutlo// AR. 1992” [Hw.] “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”; 1 ♀ (MSNG) “Montemigniaio// AR – 10c. Liconia// T. Scheffia m 863// 15.IX.05 Papileg.” [Hw.] “*Hydraena*// (s.str.) *pygmaea*// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”; 1 ♀ (MSNG) “Montemigniaio// AR. LICONIA// T. Scheffia m 841// leg Papi 29.VI.05.” [Hw.] “*Hydraena*// (s.str.) *reflexa* [sic.]/ det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”; 1 ♂ (MSNG) “PIEMONTE// illegible [Hw., faded]// Coll. Demarchi” “*Hydraena* (s.str.)// *pygmaea* Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”; 1 ♂ (MSNG) “NAVA// Alpi Maritime// 20.30-VIII-1924 F. Solari” “*Hydraena*// sieboldi// det. Doderò” [Hw.] “*pygmaea*// det. E. Pretner” [*pygmaea* Hw.] “*Hydraena* (s.str.)// *pygmaea* Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”; 1 ♀ (MSNG) “NAVA// Alpi Maritime// 20.30-VIII-1924 F. Solari” “*pygmaea*// det. E. Pretner” [*pygmaea* Hw.] “*Hydraena* (s.str.)// *pygmaea* Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”; 1 ♀ (MSNG) “BIELLA C. Code// (Sagliano) 24–9// Capellaro 58” [date Hw.] “*Hydraena* (s.str.)// *pygmaea* Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”; 2 ♂ (MSNG) “BIELLA C. Code// (Sagliano) 24–9// Capellaro 58” [date Hw.] “Rio affl.// T. CERVO” [Hw.] “*Hydraena* (s.str.)// *pygmaea* Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)” on same pin; 1 ♂ (MSNG) “Friuli// Torr. Suolrio// 2.VIII.1962.// G. Binaghi” [Hw.] “località// podestra” [Hw.] “*pygmaea*” [Hw.] “*Hydraena* (s.str.)// *pygmaea* Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”; 2 ♀ (MSNG) “Friuli// Torr. Cosizza// m. 310 Palinch// (Drenchia) [Hw.] “26.VII. 1962// G. Binaghi” [Hw.] “*pygmaea*” [Hw.] “*Hydraena* (s.str.)// *pygmaea* Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)” on same pin; 1 ♂ (MSNG) “*pygmaea*// Wather [sic.]” [Hw.] “Masaralis// Udine. 26. 3.// 52. Bucciarelli” [Hw.] “*Hydraena* (s.str.)// *pygmaea* Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”; 1 ♀ (MSNG) “Friuli// Torr. Iuolrio// m. 310. 8.VIII.// 62. Binagi” [Hw.] “località// podestra” [Hw.] “*Hydraena* (s.str.)// *pygmaea* Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”; 1 ♂ (MSNG) “Friuli// aff. Narisone// Pulfero. 22.VII.// 962. Binaghi [Hw.] “località// Lock.” [Hw.] “*pygmaea*” [Hw.] “*Hydraena* (s.str.)// *pygmaea* Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”; 1 ♂ (MSNG) “Friuli// valle Ampa// m. 650. 4.VIII.// 62. Binaghi” [Hw.] “località// Gallizzis” [Hw.] “*pygmaea*” [Hw.] “*Hydraena*

(s.str.)// pygmaea Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”]; 1 ♂ (MSNG) “Friuli// Arbida. Aff.// Torr. Cosizza” [Hw.] “m. 310. 25// VII. 1962// G. Binaghi” [Hw.] “pygmaea” [Hw.] “Hydraena (s.str.)// pygmaea Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”]; 1 ♀ (MSNG) “Friuli// Savogna. Torr.// Alberone. 23. VII.// 962. G. Binaghi” [Hw.] “pygmaea” [Hw.] “Hydraena (s.str.)// pygmaea Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”]; 1 ♂, 1 ♀ (MSNG) “REZZOAGLIO d’// AVETO (Liguria)// IX – 1918// A. Dodero” “Hydraena// sieboldi// Rosh.” [Hw.] “Hydraena (s.str.)// pygmaea Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)” on same pin; 6 ♂, 7 ♀ (MSNG) “Liguria// Rovegno. val. Treb.// bia. Rio del Riccio// m. 600. 4.V.1958// G. Binaghi” [Hw.] “Hydraena (s.str.)// pygmaea Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)” on same pin; 4 ♂ (MSNG) “Liguria// alt aval Trebbia// Rovegno. Fosso del// Riccio. M. 600. 4.// V. 1958. G. Binaghi [Hw.] “pygmaea” [Hw.] “Hydraena (s.str.)// pygmaea Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)” on same pin; 2 ♂ (MSNG) “App. Ligure// Rovegno. val// Trebbia. 16.VIII.// 60. G. Binaghi” [Hw.] “Hydraena (s.str.)// pygmaea Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)” on same pin; 1 ♀ (MSNG) “Liguria occ.// Alto (Savona)// 17.V.64. Binaghi” [Hw.] “Hydraena (s.str.)// pygmaea Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”]; 2 ♂, 1 ♀ (MSNG) “Liguria occ.// Passo Melogno// 23.IX.64. 1000// m. G. Binaghi” [Hw.] “Hydraena (s.str.)// pygmaea Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)” on same pin; 1 ♂, 2 ♀ (MSNG) “App. Tosco. Emiliano// Bosco del Teso. Campan// none. m. 1050. 16.VII.// 1959. G. Binaghi” [Hw.] “Museo Genova// Coll. Binaghi” “Hydraena// pygmaea” [Hw.] “Hydraena (s.str.)// pygmaea Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)” on same pin; 1 ♀ (MSNG) “App. Tosco-Emiliano// Bosco del Teso. Torr.// Maresca. 15.18.VII.// 959. G. Binaghi” [Hw.] “pygmaea” [Hw.] “Hydraena (s.str.)// pygmaea Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”]; 1 ♂ (MSNG) “Abruzzo// Passo Caparinelle// sorg. F. Vomano” [Hw.] 20. VII. 1878// G. Binaghi” [Hw.] “pygmaea” [Hw.] “Hydraena (s.str.)// pygmaea Waterh.// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”]; 1 ♀ (MSNG) “Cireggio// Bagnella// 28 settembre1900” [Hw.] “Hydraena// pygmaea// Sieboldi Rsnh.” [Hw., green label] “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”]; 1 ♂ (NHMW) “S Ti Brixen// Umg. Kohlen” “Teis 27.5.73// Schnekenbach” [Hw.] “pygmaea” [Hw.]; 1 ♂, 1 ♀ (NHMW) “Italia-Adamello// Val di Daone” “Hydraena// pygmaea”; 1 ♀ (NHMW) “I – Lombardia I Varese dist.// 10 km NW Varese, nr. Orino// 13.6.2001, 475 m// Komarek &

Schönmann (2)” “Hydraena// pygmaea// det. Jäch” [Hw.]; 1 ♂ (NHMW) “Abruzzo// Italien” [Hw.]; 1 ♂, 1 ♀ (NHMW) “I – Lazio(RI)// Mti della Laga// Amatrice – Capr.” “Bach in 1.400 m// 25.VIII.1992// leg. Schönmann”. **Italy, form with reflexed elytra:** 1 ♂ (NHMW) “ITALY: Calabria, 3.5 km// SW Serra San Bruno// 850 m stream” “38° 33’ 15.3”N 16° 18’ 34.8”E// 27.VIII.2018, leg. Gold-/ Schmidt (It 18-8a)” used for DNA extraction and sequencing (specimen voucher IBE-AN1129); 1 ♂, 1 ♀ (NHMW) “SILA (Calabria)// Camigliatello// VII 1933// A. Dodero” “reflexa” [Hw.] “det. E. Prettner// H. pygmaea ssp.// reflexa” [species name Hw.]; 1 ♂ (NHMW) “SILA (Calabria)// Camigliatello// “det. E. Pretner// pygmaea// reflexa Rey” [species name Hw.]; 2 ♀ (NHMW) “SILA (Calabria)// Camigliatello// 5.VIII.1933// A. Dodero”; 1 ♂ (NHMW) “SILA (Calabria)// Camigliatello// VII-VIII.1933// A. Dodero”; 1 ♂ (MSNG) “Calabria 115b 08.10.90// CS Pellegrino. Saracena.// Fte. Cannello, Quellungbach// 1385 m WE 902 040 GER” reverse “Hydraena” [Hw.] “Hydraena// (s.str.) reflexa// det. G. Ferro” “MUSEO GENOVA// coll. G. Ferro// (dono 2013)”]; 1 ♂, 1 ♀ (MSNG) “Sila (Calabria)// CAMIGLIATELLO// 25.VII. 1933// A. Dodero” [Hw.] “Hydr. Pygmaea// ssp. reflexa Rey// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”]; 1 ♂ (MSNG) “Calabria, Sila// Camigliatello// Dodero” [Hw.] “Hydr. Pygmaea// ssp. reflexa Rey// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)”]; 1 ♂ (MSNG) “Calabria, Sila// Camigliatello// Dodero” [day and month Hw.] “Hydr. Pygmaea// ssp. reflexa Rey// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)” on same pin; 4 ♂ (MSNG) “SILA (Calabria)// Camigliatello// 25.VII.1933// A. Dodero” [day and month Hw.] “H. PYGMAEA// S. REFLEXA// det. Dr. CHIESA// BOLOGNA// Via S. Stefano 1” [species name and det. Hw.] “Hydraena// s. str.// pygmaea ssp.// reflexa” [Hw.] “Hydr. Pygmaea// ssp. reflexa Rey// det. G. Binaghi” “MUSEO GENOVA// coll. G. Binaghi// (acquisto 1976)” on same pin; 1 ♂ (MSNG) “Basilicata 1093 30.09.90// PZ Pollino. Terranova.// Qu. 3 Piano delle Mandre.// 1330 m XE 073 234 GER” reverse “Hydraenidae” [Hw.] “s. reflexa// Rey// det. Ferro 1993” [species, describer and 93 Hw.].

Differential diagnosis. The short habitus, with broad, rounded elytra, together with the male leg modifications and aedeagal design make this species unmistakable with any others in the genus except *H. reflexa*. For characters separating the two species see above. With the exception of southern Italian populations, *H. pygmaea* appears to be morphologically almost uniform across its wide geographical range, including male characters (e.g. aedeagus, Fig. 4C–E).

Distribution and ecology. One of the most geographically widespread *Hydraena* in the Western Palaearctic, known throughout much of central and southern Europe and Western Asia, from Ireland to Anatolia and Armenia, and from

Scotland in the north to southern Spain, the southern Italian Apennines and the Peloponnese (Greece) in the south (Jäch & Skale, 2015). Absent from Scandinavia and North Africa. *H. pygmaea* is most common in small, stony headwater streams, where it can be found in moss and in association with clay exposures. In some areas (e.g. Bulgaria) it can also be frequent on rotting wood in streams. All specimens examined from throughout the range have been micropterous, a highly unusual finding for such a widespread water beetle (Foster et al., 2020). The species has shown evidence of decline over the past half century in the UK (Foster et al., 2020), usually in association with agricultural pollution, but also recently lost from some apparently unmodified catchments, for example at Conic Hill in Lochlomondside, Stirlingshire, Scotland.

Discussion

Our calibrated phylogeny reveals the disparate evolutionary origins of endemic Tyrrhenian Island *Hydraena*, our included species being derived from four separate colonisation events, occurring at different time periods over the geological history of these islands. All Tyrrhenian species appear to post-date the separation of Corsico-Sardinia from Palaeo-Europe in the Oligocene. *Hydraena vodozi*, which could not be included in our analyses, is morphologically closest to members of the *H. rufipes* group and therefore represents a fifth colonisation, of currently unknown timing. Our study also demonstrates conclusively that *H. reflexa* should be considered as a species separate from *H. pygmaea*, apparently endemic to the Tyrrhenian islands of Corsica and Sardinia.

The oldest *Hydraena* lineage in the Tyrrhenian Islands is comprised of the three endemic, allopatric members of the *H. holdhausi* group: *H. aethaliensis*, endemic to Elba, *H. sardoa*, endemic to Sardinia and *H. subacuminata*, endemic to Corsica. This lineage diverged from other included members of the *H. holdhausi* group ca. 14.17 Ma, according to our analysis, long after the initial separation of Corsica-Sardinia from the European continent in the Oligocene. At this time, the Langhian stage of the Mid Miocene, Corsica and Sardinia were positioned approximately where they are today, largely surrounded by shallow shelf seas adjacent to the proto-Apennines (Cornacchia et al., 2021), but with northern Corsica still potentially retaining a land connection to the southern margin of Palaeo-Europe (Meulenkamp & Sissingh, 2003). Extant Tyrrhenian species of the *H. holdhausi* lineage are apparently much younger, however, divergences between these taxa beginning at ca. 1.37 Ma in the Mid Pleistocene. Colonisation of individual islands may therefore have been facilitated by periods of lowered sea level at this time (Fattorini, 2009; Fiorentino et al., 2010; Ketmaier et al., 2006), subsequent population

isolation leading to allopatric speciation. Our phylogeny includes most western Mediterranean members of the *H. holdhausi* group, particularly those of Iberia and Morocco. Missing, however, are members of the group from elsewhere in North Africa, in particular Algeria, known to support a number of species morphologically close to Tyrrhenian taxa (Berthélemy et al., 1991). Unfortunately it is not possible to obtain Algerian *Hydraena* for molecular work at present. It should be noted, however, that their inclusion may split the long branch leading to Tyrrhenian members of the *H. holdhausi* group, which may have colonised the region from North Africa during the Messinian, when the southern coast of Sardinia was much closer to that of North Africa/Sicily (Roveri et al., 2014). The role of North Africa in western Palaearctic biogeography has become more widely appreciated in recent years, the region including important refugia for temperate biota during the Plio-Pleistocene, and being an important source area for European taxa (Husemann et al., 2014). This includes aquatic beetles, many lineages including species endemic to either side of the Mediterranean, with North African taxa often appearing relatively basal to those in Europe in phylogenies (e.g. Ribera & Reboleira, 2019).

Two *Hydraena* lineages which our calibrated analysis suggests colonised the Tyrrhenian Islands during the Messinian are endemic members of the “*Haenydra*” lineage (*H. evanescens* on Corsica and *H. rosannae* and *H. tyrrhena* on separate parts of Sardinia) and *H. reflexa*. These endemics appear to have become isolated from relatives on the European continent by events associated with the end Messinian and the subsequent Zanclean Flood, which began some 5.33 Ma (García-Castellanos et al., 2009; Krijgsman, 2002). *H. reflexa* diverged from *H. pygmaea* ca. 5.53 Ma (95% confidence interval 3.49–7.68), this date coinciding remarkably well with the Messinian Salinity Crisis (Roveri et al., 2014). Endemic “*Haenydra*” diverged from mainland relatives ca. 4.66 Ma (95% confidence interval 3.16–6.16), which again could be attributed to Messinian colonisation, when confidence intervals are taken into account. Such a conclusion was also reached by Ribera et al. (2011), albeit only including *H. evanescens*. A number of other Corsico-Sardinian endemics have been estimated to be of a similar age, including some cave salamanders (*Speleomantes*; Carranza et al., 2008), brook newts (*Euproctus*; Carranza & Amat, 2005) and the painted frog *Discoglossus sardus* (Zangari et al., 2006). The dispersal of these taxa would have required a land corridor of the type that was probably also suitable for *Hydraena*. For approximate position of key land masses during this time window see Fig. 2. Divergence between the three allopatric endemic members of the “*Haenydra*” lineage is more recent, however, being within the last ca. 2.01 Ma (95% confidence interval 1.11–2.99). As with the *H. holdhausi* group members discussed above, such events may have been triggered by Pleistocene sea level changes, as suggested by Audisio et al. (2009).

Hydraena subsequens appears to have colonised Tyrrhenian islands more recently at ca. 3.37 Ma (95% confidence interval 2.05–4.76), even confidence intervals placing this event after the Zanclean Flood. The species may have been separated from mainland relatives in the *H. nigrita* group by over-water dispersal, or sea level changes in the Pliocene–Pleistocene, which may have also resulted in its relatively wide distribution across Corsica, Sardinia and the Tuscan Archipelago. A similarly wide distribution is seen in some other Tyrrhenian taxa, including *Discoglossus sardus* (Zangari et al., 2006). Phylogeographic study of populations of *H. subsequens* in the future would clearly prove illuminating regarding its origin and colonisation history.

Hydraena pygmaea is one of the most widespread *Hydraena* species in the Western Palaearctic. This species, characteristic of small headwater streams, is known from Ireland in the west to western Anatolia (Turkey) and Armenia and in the east, and from Scotland in the north to Spain, Italy and Greece in the south (Berthélemy, 1964; Bilton, 2013; Foster et al., 2020; Jäch & Skale, 2011, 2015; Janssens, 1965; Millán et al., 2014; Spitzenberg, 2021; Valladares et al., 2018). Balfour-Browne (1958) claimed that the species was entirely wingless, but recent observations by DTB have shown that *H. pygmaea* is micropterous, no fully-winged individuals being observed in specimens examined from Britain, Bulgaria, Greece and Spain (Foster et al., 2020). This is surprising for such a geographically widespread water beetle, but fully-winged specimens, if they occur, appear to be genuinely very rare. The widespread distribution, with virtually no significant morphological or genetic divergence between populations, is very unusual, particularly in the context of the genus *Hydraena*, where recently evolved microendemics are frequent, even in fully winged lineages. COI divergences between sequenced specimens of *H. pygmaea* likely reflect survival in separate refugia during Pleistocene glacials. Whilst our geographical sampling is far from complete, the haplotype network (Fig. 2) suggests the existence of refugia in Iberia, Italy and the Balkans. In the past *H. pygmaea* has been placed along with *Hydraena minutissima* Stephens, 1829 and *Hydraena sharpi* Rey, 1886 in a separate subgenus, usually *Hadraena* Rey, 1886 (e.g. Berthélemy, 1986; Perkins, 1997). More recently, both morphological (Jäch et al., 2000) and molecular analyses (Trizzino et al., 2013a and herein) have shown that these species fall well with the subgenus *Hydraena* s.str., and that whilst *H. pygmaea* and *H. minutissima* appear closely related, *H. sharpi* belongs with other taxa of *Hydraena*.

Outside Britain and Ireland, the only islands from which *H. pygmaea* had been reliably recorded are Corsica and Sardinia. Corsican specimens had long been known to differ from those elsewhere in having a much

more strongly developed reflexed lateral margin to the elytra, particularly in females, a feature which attracted the name *reflexa*. Considered a valid species by Rey and other early workers (Kuwert, 1888; Rey, 1884; Zaitzev, 1908), *reflexa* was relegated to a subspecies of *H. pygmaea* by Orchymont (1930). Orchymont noted that Corsican beetles differed from those on the mainland on their reflexed elytra and also male leg modifications, but considered the aedeagi of these forms identical. Placing primacy on this character set, he considered *reflexa* conspecific with *H. pygmaea*, as “une race géographique de cette dernière et dérivant d’elle”. In Italy, *reflexa* has been reported from Sardinia and Calabria in the past (Binaghi, 1958; Audisio & De Biase, 2005). Despite lacking molecular data, we show that Sardinian specimens resemble those from Corsica, particularly in the distinctive form of the terminal piece of the aedeagus, confirming that true *reflexa* apparently occurs on both islands. As noted above, Corsican and Sardinian specimens differ somewhat in their male leg modifications, suggesting some independent evolution of these characters since the two populations have become isolated. *H. reflexa*-like specimens from Calabria and Basilicata, in the far southwest of the Italian Peninsula, differ from true *reflexa* on the precise form of their expanded elytral margins, which are smaller and more parallel-sided, particularly in males (Fig. 6A–B). They also have aedeagi identical to *H. pygmaea* from elsewhere in its range and as a consequence we consider them conspecific with *H. pygmaea*. On present evidence, there appear to be two possible scenarios for the evolutionary origin of this southern Italian form, which could be tested in the future with more extensive DNA sequence data. Firstly, it is possible that *reflexa*-like animals from Calabria and Basilicata may have developed their reflexed elytral margins independently of true *H. reflexa* on Corsica–Sardinia. This hypothesis is supported by the subtle differences between these characters in the two populations. Alternatively, *reflexa*-like populations in southern Italy may have arisen through past hybridization, and subsequent introgression, between a *reflexa*-type ancestor and true *pygmaea*. Whilst their remain uncertainties over the exact position and nature of land masses in the central Mediterranean over the last 10 Ma, it is clear that the Calabrian block is much older than most of the modern Apennines, and that it was situated further northwest, adjacent to modern Sardinia, during the Messinian (Rosenbaum et al., 2002b; Cornacchia et al., 2021 – see Fig. 2). At this time, given lowered sea levels, the block could readily have been colonised by *H. reflexa*, these populations subsequently interacting with *H. pygmaea* s.str. following the southeastern movement of Calabria and its connection to the nascent Apennines ca. 2 Ma (Rosenbaum et al., 2002b). Maximum COI divergence between the Calabrian specimen sequenced here and

other *H. pygmaea* is 2.73%, suggesting that these populations diverged from those elsewhere during the Pleistocene, and we assume that this either reflects the independent origin of this form, or the presence of *pygmaea*-derived mtDNA. Clearly, DNA data from a greater range of loci, including geographically close Italian populations of morphologically typical *H. pygmaea*, would prove illuminating in the future.

Our calibrated phylogenetic analysis demonstrates that *H. reflexa* is, in a comparative sense, strongly differentiated from *H. pygmaea*, the species pair showing a much higher level of sequence divergence than that observed between many other *Hydraena* sister species and indeed complexes. *Hydraena reflexa* is also shown to be distinct morphologically from the widespread *H. pygmaea*, being distinguishable on both external and aedeagal characters. As such, these two taxa are more strongly differentiated morphologically than many other species pairs or complexes in the genus. We show that whilst the male genitalia of these two species are indeed similar in overall design, there are consistent differences between them. Furthermore, the detailed morphology of the distal lobe of both species is apparently remarkably constant, including across the wide geographical range of *H. pygmaea*. Previous illustrations of the aedeagus of *H. pygmaea* are wrong on some aspects of detail, particularly in showing the gonopore-bearing flagellum curving away from the funnel-like secondary lobe of the distal lobe (e.g. Berthélemy, 1964). Having examined males from throughout the range of *H. pygmaea* we are confident that the curvature of this flagellum is relatively constant, as illustrated here. Differences between our images and previous ones may be the result of the way in which aedeagophores were treated in the past, including the use of slide mounts with coverslips and lactic acid, both of which can cause distortion to fine structures.

In short, our study emphasises the complex nature of faunal assembly on islands formed from continental terranes, focussing on a suite of related freshwater insects, a group which has been poorly studied in the region to date. We reveal a pattern of multiple colonisation events, apparently at different time windows, with a strong signal of the potential influence of the Messinian Salinity Crisis and the subsequent Zanclean Flood. We also reveal the existence of an additional Tyrrhenian endemic water beetle species, *Hydraena reflexa*, restricted to mountain streams on Corsica and Sardinia, strongly differentiated from its closest mainland relatives.

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Data availability DNA sequence data are available on GenBank, new sequences being deposited under accession numbers OR533284-OR533287, OR537346 and OR543921.

Declarations

Competing interests The authors declare there are none. The authors did not receive support from any organization for the submitted work.

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