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A new species of *Ochthebius* (*Cobalius*) (Coleoptera: Hydraenidae: Ochthebiinae) inhabiting marine rockpools of NW Sicily

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Abstract

Here we describe a new species of *Ochthebius* (*Cobalius*) from marine rockpools of NW Sicily: *O. (C.) senczuki* **sp. n**. This species was first discovered on the basis of molecular evidence, but its taxonomic distinction has been subsequently supported by morphological characters. *Ochthebius* (*C.) senczuki* **sp. n**. shows a clear genetic diversity from the known related species, with an average COI p distance ranging from 5.6% to 10.7%; it exhibits only small morphological differences, mostly limited to dorsal punctation, pronotal and elytral outer edge, and (in males) to the mobile part of the median lobe of the aedeagus. The origin of *O. (C.) senczuki* **sp. n**. is estimated to lie in the Late Miocene (~9 Mya); the ancestors of this taxon probably remained isolated from populations of the related taxa of the *Ochthebius (Cobalius) subinteger* and *O. (Cobalius) adriaticus* complexes during cycles of regressive and transgressive marine phases that occurred in the SW Mediterranean during Late Miocene and Pliocene. The detailed state of the art of members of the *O. (Cobalius) adriaticus* complex throughout the Central and Eastern Mediterranean rocky coastal areas is also preliminarily discussed.

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Keywords: Hydraenidae, marine rock pools, new species, cryptic biodiversity

Introduction

Rocky shores and marine coastal rockpools frequently host a specialized aquatic microfauna (Antonini et al. 2010; Audisio et al. 2010; Sabatelli et al. 2016, 2018, 2021a, 2021b; Rosenfeld et al. 2019; Vecchioni et al. 2019, 2021) mostly found in the supralittoral zone. Marine rockpools are extreme habitats, filled by splashes of sea water during high tides or storms, or by rain, and are highly variable in size, water depth, elevation above sea level, distance from the sea water front, average temperature, relative salinity, and the local composition and density of microalgal flora (Underwood & Skilleter 1996; Firth & Williams 2009; Firth et al. 2014). Among the invertebrates adapted to the harsh and everchanging environment of the supratidal zone, several members of the beetle family Hydraenidae, genus *Ochthebius*, are known to inhabit (at both larval and imaginal stages) the hypersaline marine rock pools along the east Atlantic, Mediterranean, Macaronesian and Southern Africa coasts (Jäch 1989, 1993; Delgado & Soler 1995, 1997; Urbanelli et al. 1996; Turner 2004; Audisio et al. 2010; Antonini et al. 2010; Sabatelli et al. 2013, 2016, 2018, 2021a, 2021b; Jäch & Delgado 2017; Ribera & Foster 2018; Ribera & Cieslak 2019; Villastrigo et al. 2020a, 2020b, 2022a, 2022b; Mirón-Gatón et al. 2022; Velasco et al. 2022), Australia (Perkins 2007; Villastrigo et al. 2019), East Asia and the west coast of North America

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(Jäch & Delgado 2014; Villastrigo et al. 2019). The genus Ochthebius Leach, 1815 (Coleoptera: Hydraenidae: Octhebiinae) includes more than 500 aquatic or semi-aquatic species worldwide, mostly distributed in Palearctic, Nearctic, and Oriental regions, with a still increasing number of new species recently discovered in almost all continents (Audisio et al. 2010; Jäch & Delgado 2017; Yoshitomi et al. 2019; Villastrigo et al. 2020b; Bilton 2021). Within this widespread genus, in the Atlantic-Mediterranean coastal areas two lineages are recorded as regular and nearly obligate colonizers of marine rockpools, i.e. members of the subgenus Cobalius Rey, 1869, and members of the "O. quadricollis group" (as recently considered by Sabatelli et al. (2016) and Villastrigo et al. (2019, 2020a, 2022b)), within the species-rich and highly diversified nominal subgenus Ochthebius s.str.

Recently, Sabatelli et al. (2016, 2021b) and Villastrigo et al. (2020b) detected the presence of a remarkable number of new NE Atlantic and Mediterranean cryptic taxa of Cobalius and of the "Ochthebius quadricollis group", clearly evidencing in both groups the presence of at least four types of "hidden" biodiversity, frequently combined with one another: (1) true cryptic species, morphologically indistinguishable, although separated by high genetic divergence based on mitochondrial markers (e.g. COI mean *p*-distance >6-7%) and difficult to discover without availability of molecular data; (2) morphologically distinct but exceptionally rare species, in most cases confused among thousands of specimens of common similar taxa, and then almost impossible to discover without massive sampling in each explored locality; (3) species with very limited geographic ranges, almost impossible to discover without an extended, complete, and careful geographic coverage of the rocky coastal areas of the whole Mediterranean basin and of the NE Atlantic, including small islands and Macaronesia; (4) species apparently specialized only to peculiar microhabitats represented by ecologically different types of marine rockpools or of other coastal salt habitats, such as below boulders in gravel and among coarse sands in the intertidal zone (Villastrigo et al. 2020b), or along the shores of salt coastal wetlands (Bennas et al. 2013) and isolated salt ponds, or even in backwaters of coastal saline streams (A. Millan, pers. comm., 2016).

This situation is particularly evident in members of the subgenus *Cobalius*, which usually exhibit higher levels of ecological specialization and geographic endemization (Villastrigo et al. 2020b; Sabatelli et al. 2021b; Mirón-Gatón et al. 2022; Velasco et al. 2022), the latter condition probably associated with a reduced dispersal ability and demographic success (Velasco et al. 2022), if compared with the frequently syntopic members of the "O. quadricollis group".

In this general scenario, as a result of recent additional research on the Ochthebius of the marine rockpools in southern Italy by Sabatelli et al. (2021b), we report here the discovery of a new morphologically and molecularly distinct species of Cobalius, O. (C.) senczuki sp. n. from NW Sicily. The new species was first detected only based on molecular evidence, but its taxonomic distinction has been subsequently supported by morphological characters. In the same study (Sabatelli et al. 2021b), using the Bayesian relaxed phylogenetic approach. the possible origin of this new species was estimated in the Late Miocene (~9 Mya). The present paper is therefore devoted to formally describing this new species of Cobalius, and to briefly discussing the state of the art of the interesting clade of Cobalius (to which our new Sicilian species could be also related) including O. (C.) adriaticus from Central and Eastern Mediterranean areas and its problematic subspecies and/or related cryptic species.

Materials and methods

Abbreviations

Abbreviations of museum institutions are as follows:

BCP—D. Bilton's collection, University of Plymouth, UK

CAR-MZUR—P. Audisio's collection, currently housed in the Zoological Museum, Sapienza Rome University, Rome, Italy

Measurements, drawings and photographs

Color photographs of the new species herein described (Figure 1) were taken in the Interdepartmental Laboratory of photo stereomicroscopy of the Sapienza Rome University (Department of Environmental Science), using a Leica® IC80 HD digital camera mounted on a Leica® M205C stereomicroscope, with a PLANAPO® 1.0× lens. The high-definition images were acquired through the LAS® v. 4 acquisition program and then processed with the Helicon Focus® 7 software package.

Measurements of adult external anatomical features were made using a digital camera mounted on a WILD® MZ8 stereomicroscope (40–80×), and the image processing software package WINVISION® (Delta Sistemi®, Rome). Photos of the male genitalia of the new species (Figure 2(a)) were obtained using



Figure 1. Holotype of O. (Cobalius) senczuki sp. n.; (a) dorsal habitus; (b) head and pronotum. Scale bars: a = 0.3 mm; b = 0.1 mm.



Figure 2. Aedeagus of *O. (Cobalius) senczuki* sp. n.; (a) (male holotype from Riserva Naturale Orientata dello Zingaro, Sicily, Italy), ZEISS® Axio Zoom V16 microscope photo, lateral view; (b) accurate drawing of the same (BX50 OLYMPUS® upright microscope, 400×), better evidencing the structure of the distal mobile lobe of the aedeagus (drawn slightly darker than reality, to better highlight its structure) and of a paramere. Scale bar: 0.1 mm.

a ZEISS®Axio Zoom V16 microscope with an APO Z® 1.5× lens, acquired through the ZEN® Toolkit acquisition software and then processed with the Helicon Focus® 7 software package. The drawing of the male genitalia of the new species (Figure 2(b)) was made with a drawing tube mounted on an a B×500LYMPUS® upright microscope (200–1000×). Measurements of tarsal, antennal, and genitalic characters were made using the same device and software.

Taxonomy: species description

Ochthebius (Cobalius) senczuki sp. n.

(Figures 1-2)

Type locality. **ITALY**: Sicily, Riserva Naturale dello Zingaro (Zingaro Nature Reserve), Trapani province, 38°05'17"N, 12°48'21"E (Figure 3).

Type material. Holotype male (CAR-MZUR) **Italy**, Sicily, Riserva Naturale dello Zingaro (Trapani province), Cala Capreria, $38^{\circ}05'17''$ N, 12° 48'21''E, 19 May 2021, S. Sabatelli & P. Audisio leg., with red holotype label. Aedeagus dissected and mounted in Euparal® on the card bearing the specimen. Not used for DNA extraction and sequencing, but for microscope photos (Figures 1 and 2). Paratypes: same locality data as for holotype, 4 November 2015, S. Sabatelli leg., 1 \Diamond (CAR-MZUR); *ibidem*, 22 May 2013, G. Senczuk leg., 1 \Diamond (CAR-MZUR); *ibidem*, S. Sabatelli leg., 4 December 2015, \bigcirc (CAR-MZUR); **Italy**, Sicily, Terrasini (Palermo province), 38°09'15"N, 13°09'28"E, 7 June 2015, S. Sabatelli & P. Audisio leg., 2 \bigcirc 1 \bigcirc (CAR-MZUR, BCP). Five additional male specimens from Sicily, Riserva Naturale dello Zingaro, 22 May 2013, G. Senczuk leg., not included in the type series, have been used for molecular analyses (Sabatelli et al. 2021b), their male genitalia having been previously dissected and preserved for morphological comparisons.

Diagnosis

A small-sized Ochthebius (Cobalius) (body length: 1.68-1.90 mm) similar in general shape to the more closely related species of the O. (Cobalius) subinteger species complex (Table I: O. (Cobalius) subinteger and O. (Cobalius) lejolisi), but characterized by other traits shared with members of the O. (Cobalius) adriaticus complex (Table I), i.e. (Figure 1, Table II) more flattened pronotum and elytra, dorsal surface between punctures rather smooth and shining, pronotal punctures separated from one another by ca. 2× their diameter, dark dorsal coloration (blackish to brownblackish with barely distinct metallic hues: Figure 1), lateral edges of pronotum very simple, with only barely distinct microscopical and blunt tegumental teeth directed outward, lateral edges of elytra with smaller, shorter and blunter tegumental teeth directed



Figure 3. Habitat of *Ochthebius (Cobalius) senczuki* sp. n. (a) Cala Capreria, Riserva Naturale Orientata dello Zingaro, Sicily, Italy; (b) Terrasini, Lungomare Peppino Impastato, Sicily, Italy.

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Table I. Genus *Ochthebius* Leach 1815, subgenus *Cobalius* Rey, 1886: list (in roughly phylogenetic order) of 18 included putative species, with recognized synonymies or homonymies (indented), as well as data on their geographic distribution. Refer to the main text for the here proposed re-evaluation at the specific rank of the three supposed subspecies of *O. adriaticus* throughout the Mediterranean. All known species are associated with marine rockpools, particularly those shallow (2–10 cm deep), small (20–70 cm wide) and positioned relatively farther from the sea (ca. up to 10 m high and inland from the sea), with the exception of the isolated *O. serratus*, present in southern Spain and northern Morocco in salty coastal wetlands and along backwaters of coastal salty streams.

Species	Distribution		
Ochthebius (Cobalius) subinteger Mulsant & Rey, 1861 Ochthebius (Cobalius) aspectabilis d'Orchymont, 1932*	Central and Western Mediterranean coasts, NW Greece, Crete Island*, coasts of W Black Sea*, ?Andaman Islands**		
Ochthebius (Cobalius) lejolisii Mulsant & Rey, 1861	Atlantic coasts of Scotland, Wales, SW Ireland, France, Iberian Peninsula, and Morocco, Mediterranean coasts of SE Spain and NW Morocco		
Ochthebius (Cobalius) senczuki sp. n.	NW Sicily		
Ochthebius (Cobalius) celatus Jäch, 1989	Italy, Sicily, Balkan Peninsula, NE Mediterranean		
Ochthebius (Cobalius) asper Sählberg, 1900	Southern continental Greece		
Ochthebius (Cobalius) adriaticus Reitter, 1886	Coasts of Adriatic Sea, southern Italy, E (and W***) Sicily		
Ochthebius (Cobalius) pleuralis Reitter, 1886 (stat. n.)	Near East (Syria, Lebanon, Israel), Crete Island		
Ochthebius (Cobalius) moreanus Pretner, 1929 (stat. n.)	Peloponnese (Southern Greece), Crete Island, Samos and Rhodes Islands (SE Greece, close to the W Turkey coast),		
Ochthebius (Cobalius) algicola Wollaston, 1871	Island of Madeira (Portugal)		
Ochthebius (Cobalius) lanthanus Ribera & Foster, 2018	Island of Gran Canaria (Spain, Canary Islands)		
Ochthebius (Cobalius) freyi d'Orchymont, 1940	Azores (Portugal)		
Ochthebius (Cobalius) balfourbrownei Jäch, 1989			
<i>Ochthebius lindbergi</i> Balfour-Browne, 1976, nec Janssens, 1961			
Ochthebius (Cobalius) gorgadensis Villastrigo, Hernando, Millán & Ribera, 2020	Cabo Verde Islands (Ihla de Santiago)		
Ochthebius (Cobalius) biltoni Jäch & Delgado, 2017	W and S Sicily		
Ochthebius (Cobalius) cortomaltese Villastrigo, Hernando, Millán & Ribera, 2020	Island of Gozo (Maltese Islands)		
Ochthebius (Cobalius) evae Villastrigo, Hernando, Millán & Ribera, 2020	Coasts of SW Spain and of NW Morocco		
<i>Ochthebius (Cobalius) anzar</i> Villastrigo, Hernando, Millán & Ribera, 2020	Island of Lanzarote (Spain, Canary Islands) and SW Morocco		
Ochthebius (Cobalius) serratus Rosenhauer, 1856	Southern Spain, N Morocco		

*We have thus far not analyzed molecularly and morphologically the populations of *O. aspectabilis* (d'Orchymont 1932), described from Crete, as well as those from any eastern Mediterranean and Pontic coastal areas attributed to *O. subinteger*; however, the possible synonymy of this taxon with the W Mediterranean populations of *O. subinteger* was confirmed by Hernando et al. (2017).

**On the contrary, as correctly believed by Ghosh et al. (2022), the records of *O. subinteger* from Indian Ocean (Andaman and Nicobar Islands, S India) reported by Jäch (1989), Hansen (1998) and recently also listed by Ghosh et al. (2022), could refer very likely to a new, undescribed cryptic species of the same complex, unless these data are based on a mistake in labeling the original material. Should new records confirm the presence of *Cobalius* sp. in the Andaman Islands, these data could introduce an interesting biogeographic scenario, including the Asian areas bordering the ancient Tethys in the range of the species of this subgenus. Other unpublished species of this lineage could therefore be discovered at least in the coastal regions of the northern Arabian Peninsula, of southern Iran and of the NW Indian subcontinent.

***As discussed in the text, it is likely that the purported W Sicilian population of *O. adriaticus* cited by Sabatelli et al. (2021b) should be referred to a distinct, undescribed species of this same complex.

outward, and slightly distinct male genitalia (Figure 2). See Table II for a list of the main characters useful to distinguish the new species from the likely more related Mediterranean taxa. Additionally, as reported by Sabatelli et al. (2021b), this new species exhibits a genetic COI mean *p*-distance (Table S1 and accession numbers MW369112–MW369174; MW369083–MW369085) between 5.6% and 10.7% from Italian (including Sicilian) and W European populations of the related *O. subinteger* and *O. lejolisii* and of ca. 6.0–7.5% from the perhaps less closely

related and markedly larger members of the *O. adriaticus* complex, including a syntopic population only tentatively referred to *O. adriaticus* (see also discussion below).

Description. Habitus (male holotype) as in Figure 1(a). Length: 1.70 mm; width: 0.62 mm. Body color uniformly shiny dark brown, with pale brown appendages. Frons without distinct microreticulation, shiny (only feeble traces of isodiametric meshes close to the eyes), and with two distinct symmetrical and Table II. Comparative table of the main diagnostic characters of *Ochthebius (Cobalius) senczuki* sp. n. In relation to other members of the more closely related Mediterranean species or species complexes (the *subinteger* and *adriaticus* complexes) of *Cobalius. O. (C.) celatus*, which based on external morphology should be attributed to the *O. (C.) subinteger* complex (Jäch 1989), exhibits quite distinct male genitalia more recalling those of members of the *O. (C.) adriaticus* complex (Jäch 1989; Villastrigo et al. 2020b), as well as a molecular positioning fully confirming its closer genetic relationships with the latter complex (Villastrigo et al. 2020b; Sabatelli et al. 2021b). For these combined reasons it is here considered separately from both the *subinteger* and *adriaticus* complexes. For our estimated values of COI genetic distances among the same taxa, see table S1 herein.

Characters	senczuki	subinteger complex	celatus	adriaticus complex
1	Outer lateral edges of pronotum with only barely distinct, small and obtuse teeth (Figure 1)	Outer lateral edges of pronotum with a series of distinct, very small triangular teeth	Outer lateral edges of pronotum with a series of distinct, very small triangular teeth	Outer lateral edges of pronotum without distinct teeth, almost simple
2	Lateral sides of elytra with a moderately wide flattened area, its middle portion ca. 0.8–0.9× as wide as width of the last antennomere (Figure 1)	Lateral sides of elytra with a rather narrow flattened area, its middle portion ca. $0.6-0.7 \times$ as wide as width of the last antennomere	Lateral sides of elytra with a rather narrow flattened area, its middle portion ca. $0.6-0.7 \times$ as wide as width of the last antennomere	Lateral sides of elytra with a wide flattened area, its middle portion ca. 1.0 up to ca. 1.5× as wide as width of the last antennomere
3	Lateral sides of pronotum with a wide, rather flattened area, also partially extended in posterior fourth (Figure 1)	Lateral sides of pronotum with a moderately wide, rather flattened area in anterior two thirds, not also extended posteriorly	Lateral sides of pronotum with a moderately wide, rather flattened area in anterior three fourths, not also extended posteriorly	Lateral sides of pronotum with a wide, rather flattened area, also partially extended posteriorly
4	Pronotum usually with space between punctures distinctly smooth and shiny (Figure 1)	Pronotum usually with space between punctures at least to some extent distinctly shagreened and dull	Pronotum usually with space between punctures at least to some extent distinctly shagreened and dull	Pronotum usually with space between punctures predominantly or entirely smooth and shiny
5	Pronotum usually with punctures fine and shallow, separated from one another by a distance markedly wider than their diameter (Figure 1)	Pronotum usually with punctures rather variable, coarse and granulose, sometimes even hardly distinct from one another, or separated from one another by a distance slightly wider than their diameter	Pronotum usually with variable punctures, sometimes rather coarse and granulose, sometimes separated from one another by a distance slightly wider than their diameter	Pronotum usually with punctures fine and shallow, separated from one another by a distance markedly wider than their diameter
6	Dorsal color usually dark brown to blackish, with only barely distinct metallic- green hues (Figure 1)	Dorsal color usually with markedly distinct metallic- green hues	Dorsal color usually with markedly distinct metallic- green hues	Dorsal color usually dark brown to blackish, rarely with barely distinct metallic-green hues
8	Posterior tibiae in both sexes rather slender, ca. 8.5× as long as wide (Figure 1), their length ca. 0.9× the maximum width of the head (Figure 1)	Posterior tibiae in both sexes moderately slender, ca. 7.5× as long as wide, ⁽¹⁾ their length ca. 0.9× the maximum width of the head	Posterior tibiae in both sexes moderately slender, ca. 7.5× as long as wide, ⁽²⁾ their length ca. 0.9× the maximum width of the head	Posterior tibiae in both sexes markedly slender, ca. 9.0– 9.5× as long as wide, their length ca. 1.0–1.1× the maximum width of the head
9	Mobile lobe of the aedeagus in males digitiform, more or less distinctly narrowed distad, and never curved dorsally if observed in lateral view (Figure 2)	Mobile lobe of the aedeagus in males digitiform, more or less distinctly narrowed distad, and never curved dorsally if observed in lateral view (Figs 5–6 in Jäch 1989)	Mobile lobe of the aedeagus in males widely sickle- shaped and subtruncated distad, very distinctly widened before apex, and rather strongly flat- widened and curved dorsally if observed in lateral view (Fig. 7 in Jäch 1989)	Mobile lobe of the aedeagus in males sickle-shaped, more or less distinctly widened distad, and more or less distinctly curved dorsally if observed in lateral view (Fig. 1 in Jäch 1989)
10	Body length: 1.7-1.90 mm	Body length: 1.7-2.0 mm	Body length: 1.7-2.0 mm	Body length: 2.0–2.8 mm

elongate foveae between eyes; with sparse setiferous punctures associated with short, thick silvery setae. Surface of clypeus and labrum shiny, with very sparse punctation and with setae shorter and finer than on frons; anterior margin of labrum evenly arcuated, in the middle with a barely distinct sinuosity. Eyes large, prominent. Without ocelli.

Pronotum (Figure 1(a,b)) hexagonal, lateral margins rounded anteriorly, markedly and abruptly narrowed posteriorly, almost indistinctly, obtusely and irregularly serrated along its outer lateral edges; surface smooth and shiny, with very sparse small punctures and irregular, larger setiferous pits of irregular shape and different diameters, less dense on disk, smaller and denser laterally, separated from one another by 1-2 diameters. Anterior angles roundly obtuse, posterior ones distinct but widely obtuse; with a narrow hyaline band at anterior and posterior margins, nearly as wide as antennal club.

Elytra (Figure 1(a)) elongate, rather parallelsided, oval distad; lateral margins rather narrowly flattened, regularly and very feebly arched, serrated through their length, with very short but distinct and sharp, spaced denticles, oriented posteriorly. Surface with rather regular series of shallow setiferous punctures, with short, fine and recurved silvery setae; surface uniformly smooth and shiny, with small and irregular rugosities around punctures. Normally developed hind wings.

Legs (Figure 1(a)) elongate and slender, tibiae with rows of strong, rather long spine-like setae along their outer edge, and with a couple of long, exceptionally thin and barely visible natatorial setae.

Ventral surface. Surface of metaventrite dull, with very small and very dense setiferous punctures, separated from one another by 0.5–1 diameters, and with small meshes and distinct microreticulation between punctures. Setae rather long and silvery-golden. Abdominal ventrites i–v densely pubescent, setae silvery-golden, nearly as long as those on metaventrite, but slightly longer and more distinct close to their posterior margins. Surface with a very distinct dull microreticulation.

Aedeagus (Figure 2(a,b), lateral view) with main piece evenly curved, of uniform width, apex pointed. Distal lobe tubular, finger-like, only moderately sclerotized, with apex regularly narrowed, moderately pointed and hyaline distad. Parameres inserted near the basal third of the median lobe, not reaching its apex.

Variation. Body length: 1.70–1.90 mm, aedeagus with moderately variable mobile distal piece.

Etymology. Named after our friend and colleague Gabriele Senczuk (zoologist at the University of Molise, Italy), who first collected this species during a herpetological survey in SW Sicily.

Distribution. Only known from the extreme NW portion of Sicily, along rocky coastal areas between the SW Palermo Province and the NW Trapani province.

Habitat. All known specimens of the new species from both Riserva Naturale dello Zingaro and Terrasini were collected in small (ca. 15–50 cm wide) and shallow (ca. 2–15 cm deep) marine rockpools (together with a few specimens of *O*. sp. cfr. *adriaticus* and several specimens of the common *O. quadricollis*), between ca. 2 and 5 m a.s.l., on calcareous rocks (Figure 3).

Comments on the state of the art of taxonomy and evolutionary relationships of members of the Ochthebius (Cobalius) adriaticus species complex

As discussed above, O. (C.) senczuki sp. n. was collected in the company of a few specimens morphologically referable to a putative population of O. adriaticus. But the latter exhibits a genetic COI mean p-distance between 3.6% and 4.4% from other Italian populations of the "true" O. adriaticus Reitter, 1886 (including those from E Sicily, the previously westernmost known populations of this taxon, if we exclude our unexpected record from W Sicily, Zingaro: see Sabatelli et al. 2021b and discussion below). This data allows us to hypothesize the possible existence of a further distinct and allopatric cryptic species of this complex in the same locality of the extreme NW Sicily. This situation has suggested to us to deepen some aspects, at the moment still rather problematic, of the evolutionary, biogeographical and taxonomic relationships involving the whole complex of species, widely distributed in most parts of the Central and Eastern N Mediterranean (Jäch 1989; Villastrigo et al. 2020b, 2022). In addition to the probably related O. (C.) senczuki sp. n. and the possible second new syntopic species just mentioned, the relations between the presumed oriental subspecies of O. adriaticus are in fact unclear and confusing.

The latter typical present-day subspecies (*O. adriaticus* s.str.) was described (Reitter 1886) from Croatia (Pula, Istria County), and it was later reported from most of the Adriatic and Jonian coasts of Italy, Slovenia, Croatia, Albania, NW Greece, and E Sicily (Jäch 1989). In the same

paper Reitter (1886) also published as a distinct species O. (C.) pleuralis from the Near East ("Syrien", probably a locality in the coastal areas of the present-day SE Turkey, Syria, Lebanon or Israel); further reports of this taxon are from Israel and from Crete Island (S Greece: Villastrigo et al. 2022). This taxon has long been considered of a synonym or an eastern subspecies O. adriaticus (Jäch 1989). A third possible subspecies of O. adriaticus was later described by Pretner (1929) from Peloponnese (S Greece) under the name O. (C.) adriaticus moreanus, and several records of this taxon were later reported from eastern continental Greece, Crete Island, and Samos Island (close to the Aegean coasts of W Turkey) (Jäch 1989; Villastrigo et al. 2022). It is interesting to highlight the recently recorded presence in sympatry in Crete of both O. adriaticus moreanus and O. adriaticus pleuralis (Villastrigo et al. 2022; presence confirmed also by our research team: unpublished data, June 2023), which strongly suggests that these two taxa, as well as very likely the allopatric O. adriaticus s.str., should represent distinct biological species, despite their rather low respective genetic distances (Villastrigo et al. 2020b, 2022). We have therefore introduced this tentative taxonomic framework in our Table I above, where we decided to formalize (subject to further molecular data that may eventually modify our conclusions) the new taxonomic state of these three taxa. A clearer and more complete scenario for this puzzling species complex could be likely obtained from further molecular and morphological analyses carried out on populations of O. (Cobalius) adriaticus s. 1. from coastal sites in the N Mediterranean, from western Sicily to Israel, to better clarify the occurrence and co-occurrence of the different known and unknown members of this group, as very appropriately discussed by Jäch (1989).

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Supplementary data

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