

Research articleSubmitted: April 20th, 2018 - Accepted: November 24th, 2018 - Published: December 31st, 2018**Biodiversity of the endangered coastal beetle *Scarites laevigatus*: is the northern Adriatic population a geographical subspecies or a case of introgressive hybridisation? (Coleoptera: Carabidae)**

Lorenzo ZANELLA

Natural History Museum Venice - Santa Croce 1730, IT-30135 Venezia, Italy - lorenzo.zanella@libero.it

Abstract

The ground beetle *Scarites laevigatus* Fabricius, 1792 is a specialized predator occurring in the Mediterranean sandy shores, currently threatened with disappearance due to the widespread modification of beach ecosystems. The present study purposes a morphological analysis of the northern Adriatic form, described by Puel in 1938 as a subspecies with the name *venetianus*, in comparison with the typical form of this taxon and *S. terricola*. The examination of pronotum, elytra, body shape, male genitalia and wing development, suggests that the studied population is different from the nominotypical form and might originate from the introgressive hybridisation of *S. terricola* with the north Adriatic populations of *S. laevigatus*. This hypothesis is discussed in the light of current knowledge of the systematics and ecology of the putative parent species.

Key words: Dune-beach ecosystem, ecological indicator, speciation, Scaritina, morphometry, gene flow.

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Introduction

Scarites (Parallelomorphus) laevigatus Fabricius, 1792 is a psammo-halobious carabid occurring in sandy shores of the Black Sea, Mediterranean and Iberian Atlantic coasts (Balkenohl 2003). This insect is specialised in preying amphipods of the intertidal and supralittoral zones, and its low tolerance to disturbances of the sandy beach environment makes it an efficient ecological indicator (Zanella et al. 2009; Conti 2017; Conti et al. 2017). Due to recent widespread changes in sandy shore ecosystems (De-feo et al. 2009), its survival is seriously threatened, with Italian populations in particular showing a severe decrease in abundance (Conti et al. 2004, 2012; Zanella et al. 2017).

In the past, the morphological variation of this species across its geographical range suggested the occurrence of local subspecies. Elytral striae were considered a pivotal diagnostic feature, since they are shallow in the nominotypical form but quite impressed in some local populations. Bonelli (1813: 475) described a subspecies characterised by deep elytral striae from the French coast close to Toulon, with the name *telonensis*. This subspecific name was later used improperly by many authors to designate other populations showing a similar morphologic character but occurring along the Adriatic coast (Porta 1923; Müller 1926; Luigioni 1929: 52). Puel (1938: 75) revised the issue, reducing *telonensis* to an infrasubspecific form of *laevigatus*

and describing a new subspecies with the name *venetianus*, occurring in some north Adriatic localities: Monfalcone, Grado and Lido of Venice (Veneto and Friuli Venezia Giulia regions). This nomenclatorial act was overlooked by most of the later authors, who maintained the name *telonensis* for the north Adriatic form (Focarile 1959; Magistretti 1965; Ratti 1986). At the end of the 20th century, both subspecies names were synonymised with the nominotypical *laevigatus* (Vigna Taglianti 1993; Balkenohl 2003).

The present study was primarily aimed at showing that the morphological analysis conducted by Puel was correct and that *S. laevigatus venetianus* can be unequivocally distinguished from the nominotypical form. Secondly, a comparative morphological analysis is proposed showing that *S. l. venetianus* might originate from the introgressive hybridisation of *S. terricola* with the north Adriatic populations of *S. laevigatus*. The findings confirm the importance of including this taxon in programs for the protection of species at high risk of extinction.

Methods

Abbreviations:

S.l.=*Scarites laevigatus laevigatus*; *S.t.*=*Scarites terricola*;
S.l.v.=*Scarites laevigatus venetianus*.

All the studied specimens were photographed and their

biometric measurements collected using the ImageJ - NIH software v. 1.45s (<http://rsb.info.nih.gov/ni-image>). Data were collected with ± 0.1 mm precision, considering the following biometric variables:

- total length (TL), from median tooth of labrum to elytral apex;
- anterior pronotum width (APW), distance between anterior-lateral angles of pronotum;
- maximum pronotum width (MPW);
- posterior pronotum width (PPW), distance between posterior angles of pronotum;
- pronotum length (PL), along midline;
- elytral length (EL), from apex of scutellum to apex of elytra;
- elytral base width (EBW), measured between humeral teeth;
- maximum elytral width (MEW).

The following morphometric indices were calculated from the biometric data in order to establish variations of shape:

- the “MPW:PL ratio”, which defines the shape of the pronotum (more or less square);
- the “EL:MEW ratio”, which defines the slenderness of the elytra;
- the “EL:PL ratio”, which defines the proportion in length between elytra and pronotum.

Statistical analysis of biometric variables and morphometric indices was performed by one-way ANOVA with permutation test and post-hoc Tukey’s HSD permutation test (9999 permutations) (Software B1SCLASSIC v. 2, SISSAD, Italy). Multivariate analyses, consisting of Principal coordinates analysis (PCoA) and one-way PERMANOVA (9999 permutations) were performed using PAST ver. 3.14 (Hammer et al. 2001).

Morphological analysis was completed by examining male genitalia and wings from 10 specimens per taxon; *S.t.* and *S.l.v.* were sampled from material collected along the

north Adriatic coast, whereas nominotypical *S.l.* (which does not occur in the same area) was sampled from the Tyrrhenian coast (Italy), Greece and Tunisia. Following a preliminary investigation, *S.l.v.* showed wing dimorphism depending on the year of collection. In order to detect possible variation in wing morphology over time, the number of examined specimens of *S.l.v.* was doubled and arranged in two groups based on year of collection: 1947-1956 vs 2014-2017. Wing length (WL) was measured as the distance from the base of the costal vein and wing apex, and then normalised on TL (WL:TL).

Entomological material examined (see appendix 1 for details):

- *S.t.* 69 specimens from Italy, 2 from France.
- *S.l.* 5 specimens from Spain; 4 from France; 109 from Italy, 13 from Greece; 20 from Tunisia.
- *S.l.v.* 250 specimens from Italy (north Adriatic coast from the Volano mouth of the Po river delta to the Tagliamento river mouth).

The material is housed at the collections of the Natural History Museum of Venice and author’s private collection.

Results

Biometrics

Table 1 shows the biometric averages (\pm standard errors) for the three taxa of interest and the related ANOVA with permutation results. *S.t.* is clearly distinct from the other two taxa based on its larger size and more parallel-sided body shape. On average, whereas *S.t.* is 23.5% longer than *S.l.*, its width of pronotum (MPW) and elytra (MEW) are only 12.2% and 15% greater, respectively. This means that *S.t.* is proportionally more slender than *S.l.*, especially with regard to pronotum.

S.l.v. is 2.6% longer than *S.l.*, on average, and therefore very similar in size. However, this small but statistically

Table 1. Biometric data \pm standard error (expressed in mm) arranged by taxon. Statistical symbols concerning differences between data groups: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; n.s. = not significant

| Taxon (n.) | TL | APW | PPW | MPW | PL | EBW | MEW | EL |
|-------------------------|------------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|------------------------|
| <i>terricola</i> (71) | 18.07 \pm 0.12 | 4.43 \pm 0.03 | 4.74 \pm 0.04 | 5.33 \pm 0.04 | 3.95 \pm 0.03 | 4.64 \pm 0.03 | 5.58 \pm 0.04 | 10.06 \pm 0.06 |
| <i>venetianus</i> (250) | 15.01 \pm 0.05 | 3.88 \pm 0.01 | 4.14 \pm 0.01 | 4.67 \pm 0.02 | 3.40 \pm 0.01 | 3.91 \pm 0.01 | 4.87 \pm 0.01 | 8.38 \pm 0.03 |
| <i>laevigatus</i> (151) | 14.63 \pm 0.06 | 4.00 \pm 0.02 | 4.20 \pm 0.02 | 4.75 \pm 0.02 | 3.33 \pm 0.02 | 3.99 \pm 0.02 | 4.85 \pm 0.02 | 8.04 \pm 0.04 |

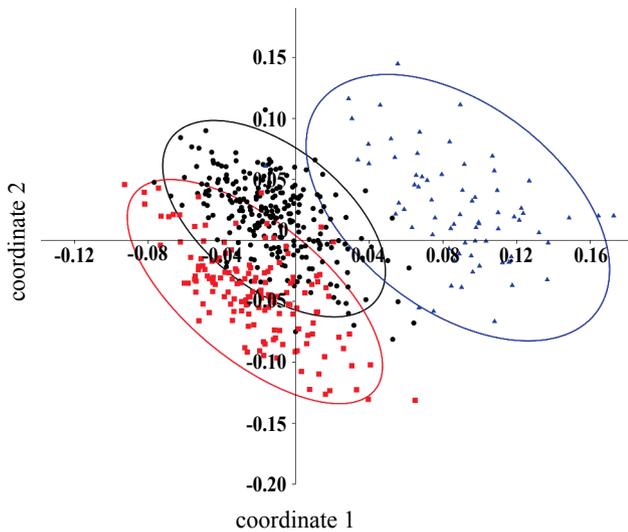


Figure 1. Principal Coordinates Analysis of the biometric data of *S.l.* (red squares), *S.l.v.* (black dots) and *S.t.* (blue triangles). Ellipses delimitate 95% confidence of each group of data.

significant increase in TL ($p < 0.001$; Tab. 1) is not accompanied by a proportional increase in body width, which is slender. This is particularly obvious in the *S.l.v.* pronotum, which is narrower by 1.7% (MPW) to 3.1% (APW) with respect to that of *S.l.* On the other hand, whereas the average EL of *S.l.v.* is 4.2% greater than that of *S.l.*, MEW shows a not significant difference (+0.4%). Therefore, the biometrics suggest that *S.l.v.* is very close in size to *S.l.*, but also possesses some body shape traits that make it resemble *S.t.*, i.e. the pronotum less transverse and elytra proportionally slender.

A multivariate graphical representation of similarity/distance between the samples by principal coordinates analysis of the biometric data is shown in Fig. 1. Coordinate 1 accounts for 95.4% of variance, whereas coordinate 2 for 2.4%. Ellipses delimit the 95% confidence interval for the data of each taxon. This graphical elaboration makes evident that *S.l.v.* data are scattered in the intermediate space between those of the other two taxa, however, consistently with the results above, *S.l.v.* shows a greater overlap with *S.l.* than with *S.t.* Multivariate analysis by PERMANOVA confirmed a statistical significance of the biometric differences between the three taxa (Bonferroni corrected p -value = 0.0003).

Biometric indices allow for a better appreciation of the differences in body shape between the three taxa (Fig. 2). *S.t.* shows the smallest ratio between width and length of pronotum, the greatest ratio between length and width of elytra, as well as the greatest ratio in length between elytra and pronotum. Therefore, *S.t.* is a little more slender than the other two taxa, with the elytra contributing more than the pronotum to the difference in TL. Whereas *S.l.* shows index values at the opposite extremes of each range, *S.l.v.* lies in an intermediate position.

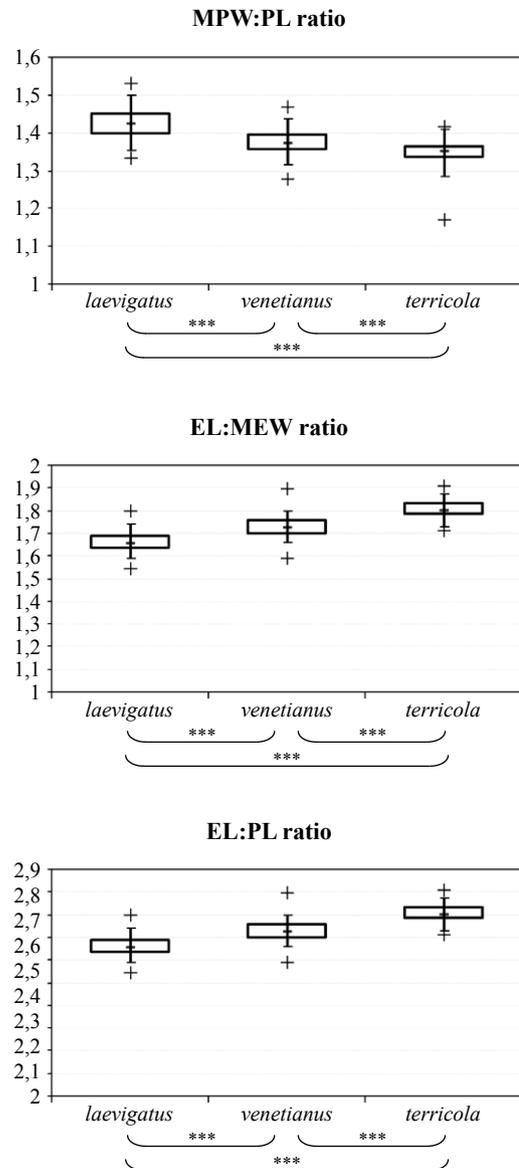


Figure 2. Box & Whisker plots of biometric indices. The short line within the box represents the median of the given variable, and the bottom and top edges the 25th and 75th percentiles, respectively (i.e. 50% of the data fall within the box). The “whiskers” extend to the 5th and 95th percentiles. Finally, the minimum and maximum values in the sample are indicated with a ‘+’ sign. Statistical symbols concerning differences between data groups: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; n.s. = not significant

Morphology

A number of external features that distinguish the three taxa can be observed on the pronotum and elytral base. *S.t.* generally presents lateral margins of the pronotum that are less curved than those of *S.l.*; the basal border in correspondence of the peduncle is always straight and maintains a regular section throughout its extent (see the arrow pointing down in Fig. 3a). Although the shape of the pronotum is less square in *S.l.*, especially concerning the curvature of the lateral margins, the taxon is fairly variable,

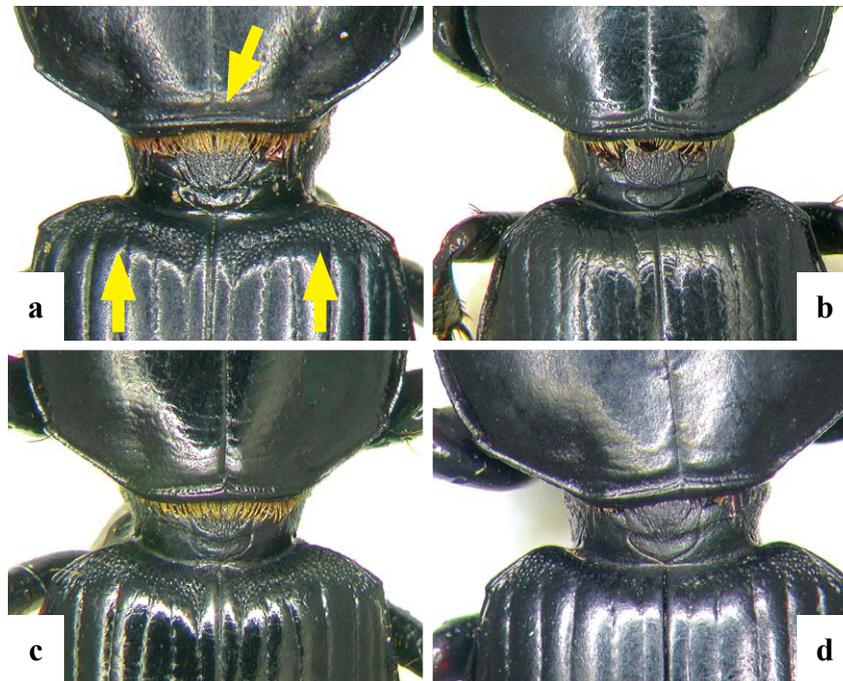


Figure 3. Middle body sections of: a) *S.t.* from Sacca Scardovari (RO), 1996; b) *S.l.* from Varano island (FG), 1987; c) *S.l.v.* from Alberoni, 2014; d) *S.l.v.* from Alberoni, 1947. Arrows point to key characteristics.

with some populations closer to *S.t.* than others. However, the basal border of the pronotum in correspondence of the peduncle in *S.l.* is slightly enlarged in the middle, where it meets the pronotal median line (Fig. 3b). This latter characteristic is also observed in *S.l.v.* (Fig. 3c-d).

In *S.t.* the elytral base is impressed and finely granulated (see arrows pointing up in Fig. 3a), with a few umbilical setiferous tubercles, small but distinguishable on the granulated background, scattered in correspondence of intervals 2-4. Elytral striae are deep from the basal tract and are finely punctured, not extending to the granulated basal area. Intervals are subconvex.

S.l. elytra are more ovate, with the base lacking an impressed area and granulation only at humeri (Fig. 3b). A small and isolated spot of fine granulation is sometimes present at the base of the first stria. Although the elytral base lacks umbilical setiferous tubercles, some specimens show two small basal setiferous punctures in correspondence of striae 1-4. Striae are fine and very shallow, imperceptibly punctured and progressively vanishing at the basal tract. Some populations show elytral striae that are more impressed, although never as deep as in *S.t.* Intervals are always flat.

The distinctive characteristic of *S.l.v.* is that the elytral base is not impressed, as in *S.l.*, but is rather continuously granulated between humeri and suture (Fig. 3c), as in *S.t.* However, although this trait is always present, *S.l.v.* shows significant variability among specimens of the same population, with some very close to typical *S.l.*, as observed by Puel (1938), especially among the oldest specimens. The

basal granulation of the elytra narrows in correspondence of intervals 3-4, sometimes becoming barely visible. The umbilical setiferous tubercles, typical of *S.t.*, are generally lacking from the elytral base, although sometimes a few can be observed in specimens that are more similar to *S.t.* The elytral base is proportionally wider and the striae more deep than in typical *S.l.*, with intervals from subconvex to almost flat. On the whole, *S.l.v.* presents a body shape that is more similar to *S.l.*, but that also shows some traits resembling those of *S.t.* Notably, specimens collected in the last few decades exhibit a more pronounced basal granulation and deeper elytral stria (Fig. 3c), as a percentage, than specimens collected before 1960 (Fig. 3d), which comprise most of the material examined.

Whereas wings are functional in *S.t.* (Fig. 4a), they are reduced in *S.l.* (Fig. 4b). WL varies with TL, but the WL:TL ratio exhibits limited variation within each taxon. Notably, *S.l.v.* shows an intermediate condition; wings are not functional but are more developed than those of *S.l.* In this taxon, WL also varies with sampling year, with the wings of recent specimens more developed (Fig. 4c) than those collected before the 1960s (Fig. 4d). Fig. 5 shows that the WL:TL ratio differs between the three taxa and also between the two subsets of *S.l.v.* collected about 60 years apart.

Finally, all taxa present male genitalia of similar morphology; no useful distinguishing features were observed (Fig. 6). This suggests that reproductive isolation based on a species-specific genital lock-and-key system is improbable.

Discussion

Puel (1938) described *S.l.v.* as being characterised by impressed elytral striae, often as deep as those in *S.t.*, with interstriae varying from almost flat to sub-convex, and an elytral base finely and uninterruptedly granulated between the humeri and basal suture of the elytra, with attenuation at the base of the 3rd and 4th interstriae. The present study validates Puel's description, confirming that this taxon should be considered a valid subspecies. The overall biometric and morphological analysis supports the conclusion that *S.l.v.* is different from the nominotypical *S.l.*, consistent with the description reported by Puel (1938), and that all its distinguishing traits confer a clear resemblance with *S.t.*

On the basis of morphological traits of pronotum and elytra, *S.l.v.* seems to be a form of passage between *S.l.* and *S.t.*, with its resemblance to the latter species showing an appreciable increase throughout the last few decades. These remarks are also consistent with observations on the wing morphology. The WL increase observed in *S.l.v.* between 1947-1956 and 2014-2017 is hardly explainable from an adaptive point of view. Although many insect taxa have secondarily lost wings and/or the ability to fly (Wagner & Liebherr 1992), the wing modifications associated with this process should not be reversible. Wing polymorphism occurs in some ground beetles, but in these cases both a fully winged form (macropterous) and a form with reduced wings (brachypterous) are observed (Aukema 1995; Dhuyvetter et al 2007). To date, *S.l.* is known to be invariably brachypterous. The less reduced wing form of *S.l.v.* could be considered a peculiarity of the north Adriatic population, but the wing elongation detected in specimens sampled from the same area a few decades later cannot be interpreted as an expression of geographical variation.



Figure 4. Wings: a) *S.t.* (Sacca Scardovari, Po River Delta, 30.VI.1996); b) *S.l.* (Orbetello, Tuscany, 5.VI.1980); c) *S.l.v.* (Alberoni, 13.VI.2017); d) *S.l.v.* (Punta Sabbioni, 5.VI.1956)

All these observations suggest the possibility that *S.l.v.* might originate from an ancestral population of *S.l.*, as a result of gene flow occurred via introgressive hybridisation with *S.t.* The pattern of morphological variation, characterized by a gradient individuals of apparent mixed ancestry, is consistent with introgression cases observed in other hybrid zones (Harrison 1986).

In the framework of this hypothesis, the increased resemblance with *S.t.*, detected by comparing specimens collected recently with others sampled in the middle of the last century, would be compatible with a greater impact of gene flow on the thinned population of *S.l.v.*, which is already locally extinct from most of the north Adriatic coast (Zanella et al. 2009, 2017).

The putative introgression needs to be confirmed through the investigation of molecular markers, however, it deserves to be taken into consideration since it would explain the reported findings and is consistent with the state of knowledge concerning phylogenesis and ecology of the parental taxa. As a first consideration, Fig. 5 suggests that

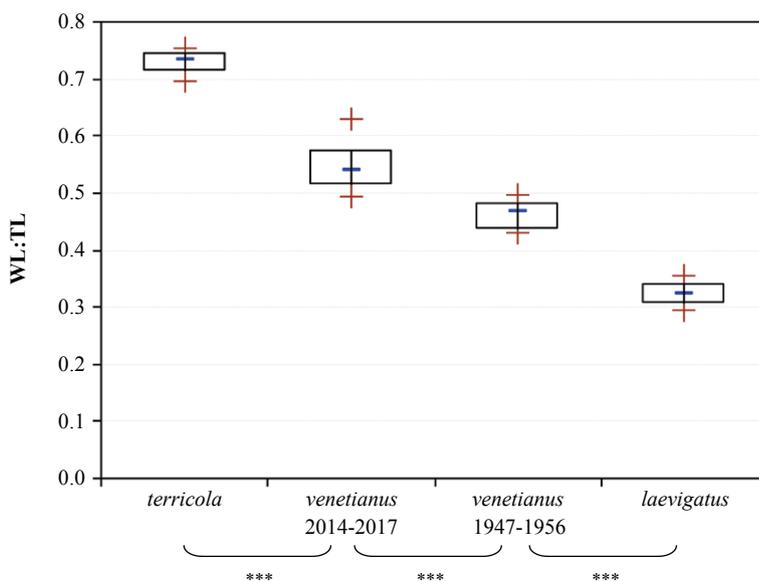


Figure 5. Box & Whisker plot of wing length normalised on total length (WL:TL). For details regarding the graphical representation see caption of Figure 2. Statistical differences between data groups: *** = $p < 0.001$.

S.l. and *S.t.* have maintained a mechanical compatibility of genital lock-and-key systems. Apart from this necessary precondition for mating success, it is known that the viability and fertility of hybrid offspring is affected by certain genetic and/or genomic traits of the parental species that could produce post-zygotic reproductive isolation (Abbott et al. 2013). However, many taxa recognised as species completely separated failed to develop a full post-zygotic isolation (Mallet 2008). In some cases, F1 hybrid gametes maintain a genetic architecture and ploidy compatible with the production of viable offspring (Lai et al. 2005; Mallet 2007). Reproductive barriers based on genomic and chromosomal mechanisms (i.e. post-zygotic) generally increase with phylogenetic distance (Orr 1995; Abbott et al. 2013; Harrison & Larson 2014), however, the two *Scarites* here considered show to be at a quite early stage of divergence. Galián et al. (1999) studied a 489 bp sequence of their mitochondrial cytochrome oxidase I gene, showing that their respective statistical distance is only 0.8%, while that to other Iberian *Scarites* was higher than 10%. On statistical basis, in Coleoptera, only 2.2% (20 cases out of 891) of congeneric species pairs show COI divergence smaller than 1%, while the mean divergence estimated is 11.2% (Hebert et al. 2003). This means that the COI divergence detected between *S.l.* and *S.t.* is comparable to the intraspecific variation of many other species.

Furthermore, these two *Scarites* share similar chromosome numbers, i.e. $56 + X$ and $60 + X$ (males have a sin-



Figure 6. Male genitalia in dorsal (left) and lateral (right) view: *S.l.* from mouth of the Ombrone river, Tuscany, 23.VI.1972 (a and b); *S.l.v.* from Punta Sabbioni (VE), 5.VI.1956 (c and d); *S.t.* from the lagoon of Venice, 27.III.1991 (e and f).

gle X sex heterosome), respectively, i.e. numbers higher than other congeneric species (Galian et al 1999). *S.l.* has two pair of very small chromosome more than *S.t.* (Galian et al 1999), perhaps originated by dissociation of ancestral chromosomes into smaller pairs, as showed to occur in some populations of *S. buparius* (Serrano 1980).

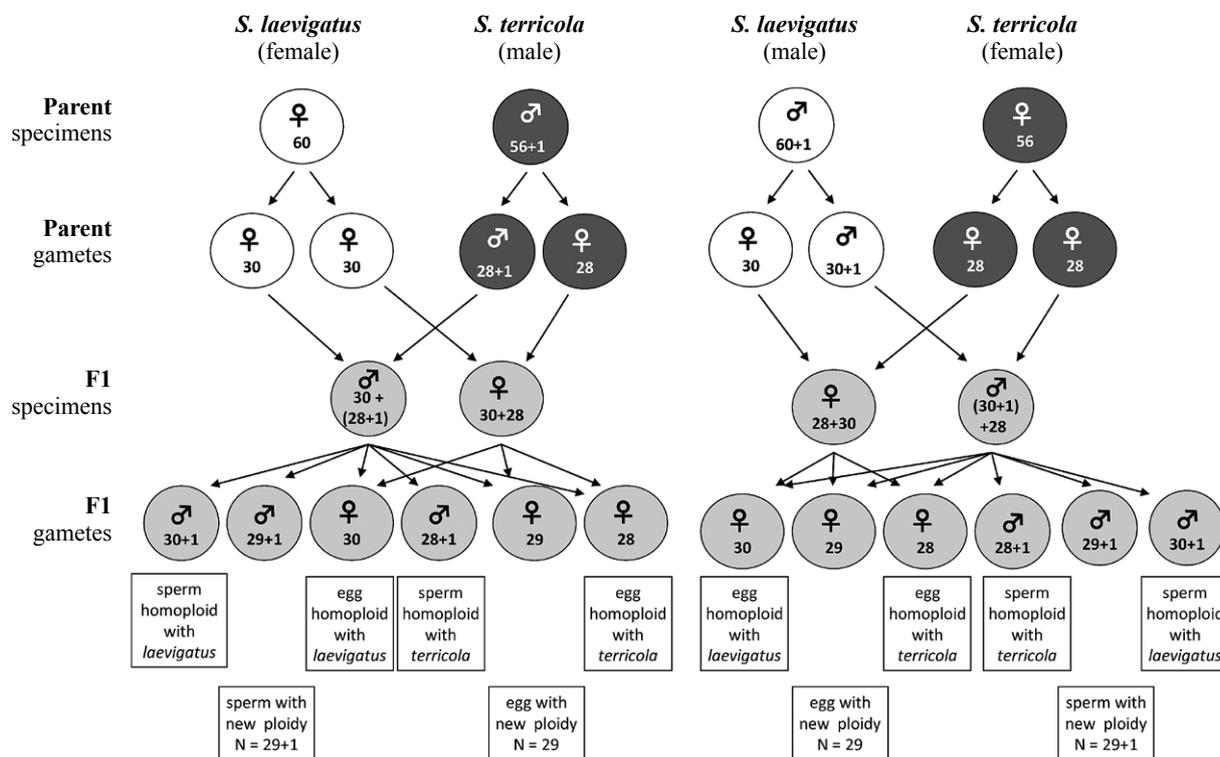


Figure 7. Diagram of chromosome numbers in the parental species, *S.t.* and *S.l.*, and partition in their respective gametes. Hypothetical chromosome numbers in different F1 hybrids and their respective gametes.

The small size of these differential chromosomes suggests that the genetic imbalance between the two species, if any, should be quantitatively small. However, the production of aneuploid gametes can be an effective reproductive barrier (ignoring speciation by polyploidy) (Mallet 2007). On this regard, despite putative F1 hybrids should be characterized by an intermediate karyotype (58 + X chromosomes), they could have the capability to produce gametes with the same chromosome numbers of the parental species, at least as part of their total gamete pool, as shown in the hypothetical scenario of Fig. 7. This scheme illustrates that F1 hybrids are potentially suitable to introduce allospecific genes into the parental genomic pool by backcrossing. Of course, many genetic and genomic incompatibilities can negatively affect the fertility of F1 hybrids (Martin & Jiggins 2017), but the production of homoploid gametes and the phylogenetic proximity of the parental genomes are elements in favour of the introgression hypothesis (for a deep analysis of F1 hybrids fertility in connection with re-combinational processes of speciation see McCarthy et al. 1995 and Buerkle et al. 2000).

As an additional comment, it should be noted that *S.t.* exhibits marked sperm dimorphism that cannot be assimilated to any type of sperm polymorphism previously known in other insect species (Sasakawa 2009). Although this finding has no obvious relationship with the hybridisation potentiality of *S.t.*, it does suggest that this taxon is characterised by a reproductive biology that is at least partially unknown. Besides, such sperm dimorphism could directly affect gametic compatibility with the eggs of close species.

It is recognized that divergent ecological specialization is a major driver in sympatric and parapatric speciation (Rundel & Nosil 2005) and it is worthy to remark that *Scarites* in discussion occur in adjoining habitats.

S.l. is a halobiont with low dispersal ability, inhabiting well preserved sandy seashores, where, before the current problems of conservation, it occurred in dense populations (Contarini 1838; Ragusa 1883) along the wet or semi-humid sandy belt between the intertidal zone and white dunes (Zanella et al. 2009; Conti et al. 2012). In contrast, *S.t.* is a halophilous flying carabid that typically inhabits various coastal environments characterised by sandy or sandy-loamy soils, but which is also sporadically recorded from continental riparian habitats (Magistretti 1965; Wiezik 2005; Rogatnykh & Koshki 2011). Along the north Adriatic coast, *S.t.* is usually found in diffuse, low-density populations across soils with low salinity, such as reclaimed lands and retrodunal biotopes (Ratti 1986; Zanella 2010; Zanella & Scarton 2017). Therefore, although these two taxa show different habitat preferences, their respective populations are often very close and susceptible to enter in contact. On this regard, the several hundred thousand hectares of saline wetlands scattered along the NE Adriatic coast between Ravenna (FE) and the Gulf of Trieste offer unique conditions for extensive contact between *S.t.*

and *S.l.* Indeed, sporadic specimens of *S.t.* were at times observed in sympatry with *S.l.* on the sea beaches of Venice Lido (San Nicolò 13.IX.2014, 1 specimen; Alberoni 12.VI.2017 and 13.VII.2017, 2 specimens; leg. L. Zanello). These observations attest that *S.t.* can occasionally migrate (possibly by flight) towards the typical habitat of *S.l.* and that mating could potentially occur.

The ecological relevance of *S.l.*, currently endangered, as well as the scientific interest regarding the role of hybridisation in speciation, which is still insufficiently understood, make this putative case of introgression worthy of further investigation, in particular by means of a molecular approach.

Acknowledgements – I am greatly indebted to Marco Uliana (Museum of Natural History of Venice) for his scientific support and critical revision of the manuscript. I am grateful to Paolo Pertile (Cutech Srl) who made available the statistical software used to process data.

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Appendix 1. Material examined.

Scarites laevigatus laevigatus

| Country (Region) | Locality | Date | Specimens |
|--|---|--------------|-----------|
| IT (Liguria) | Sacca di Magra Sarzano (SP) | 6.VI.1954 | 1 |
| IT (Tuscany) | San Vincenzo (LI) | 26.VII.1981 | 2 |
| | mouth river Ombrone | 23.VI.1972 | 6 |
| | | 6.VI.1980 | 2 |
| | Litorale Cecina (LI) | 8.V.1976 | 15 |
| | M.ts Uccellina (GR) | VIII.1966 | 6 |
| | M.ts Uccellina,Torre Collelungo (GR) | 6.IX.1969 | 1 |
| | Orbetello (GR) | 5.VI.1980 | 15 |
| IT (Lazio) | Castelfusano (RM) | VII.1955 | 1 |
| | Passo Oscuro (RM) | 5.VI.1958 | 8 |
| | Lido of Rome | 15.VI.1934 | 6 |
| | Fogliano (LT) | V.1953 | 1 |
| | Minturno (LT) | IX.1952 | 3 |
| IT (Apulia) | Gargano Rodi (FG) | 30.V.1948 | 1 |
| | Gargano S. Menaio (FG) | 5.I.1960 | 1 |
| | Isola Varano (loc. Iale) (FG) | 25.VI.1987 | 2 |
| | Leuca (LE) | 5.I.1960 | 1 |
| | Punta Maculone (LE) | 25.IV.1948 | 11 |
| | | 30.IV.1948 | 1 |
| | Taranto | 30.V.1951 | 3 |
| IT (Basilicata) | Scanzano (MT) | 23.VI.1982 | 1 |
| IT (Calabria) | mouth river Crati | 31.V.1980 | 6 |
| | Tropea (VV) | 1981 | 1 |
| IT (Sicily) | Idria (ME) | 23.IX.1954 | 1 |
| | Messina | - | 1 |
| | Messina Torre Faro | IV.1973 | 1 |
| | Piano Torre (ME) | IV.1951 | 4 |
| | Siracusa | 21.V.1966 | 1 |
| | Spadafora (ME) | 2.VI.1951 | 3 |
| | Taormina (CT) | 9.VIII.1977 | 1 |
| | Cefalù (PA) | 10.IV.1957 | 1 |
| IT (Sardinia) | Arborea (CA) | 15.V.1951 | 1 |
| GR (Crete) | Iraklion | 10.VII.1979 | 5 |
| GR (Macedonia) | Kavala | 28.VI.1991 | 5 |
| GR (Rhodes) | Rhodes | 21.VI.1964 | 2 |
| GR (Peloponnese) | Githio (Sparta) | 9.IV.2003 | 1 |
| ES (Andalusia) | Cabo de Gata (Almeria) | 13.VIII.1977 | 1 |
| | | 26.VII.1987 | 2 |
| ES (Murcia) | Capo de Palos (Carthagenia) | 22.VI.1954 | 2 |
| FR (Provence-Alpes-Côte d'Azur et Occitanie) | Beaduc | 15.VII.1955 | 4 |
| FR (Occitanie) | Plage de Sète | 23.V.1952 | 1 |
| TN (Jendouba gov.) | Tabarka | 17.VI.1951 | 3 |
| | | 18.VI.1951 | 9 |
| TN (Sfax gov.) | 10 km S of Sfax | 12.VI.1951 | 3 |
| TN (Nabeul gov.) | Cap Bon | 9.VI.1951 | 1 |
| TN (Tunis gov.) | El Marsa | 8.IV.1954 | 1 |
| AG (Oranie) | Plage Port aux Poules (Marsat El Hadjadj) | 24.VI.? | 1 |
| MO (Casablanca-Settat) | Fedalah | 27.VI.1951 | 1 |

Scarites laevigatus venetianus

| Country (Region) | Locality | Date | Specimens |
|----------------------------|-----------------------------------|---------------|-----------|
| IT (Friuli Venezia Giulia) | Lignano (Tagliamento river mouth) | 6.VII.1982 | 1 |
| IT (Veneto) | Marina di Eraclea (VE) | 25.VI.1967 | 1 |
| | | 30.VIII.1967 | 1 |
| | Jesolo Lido (VE) | 6.VII.1954 | 3 |
| | | 2.VI.1960 | 1 |
| | | 14.XII.1960 | 1 |
| | | 20.VI.1961 | 2 |
| | | 25.VI.1961 | 2 |
| | | 7.VII.1962 | 1 |
| | | 5.VII.1963 | 2 |
| | | 6.VII.1963 | 1 |
| | | VII.1964 | 1 |
| | Punta Sabbioni (VE) | 1.VII.1950 | 4 |
| | | 24.VII.1953 | 1 |
| | | 7.VIII.1954 | 1 |
| | | 06.VI.1956 | 28 |
| | Lido of Venice | 17-18.VI.1938 | 1 |
| | | 24.IV.1946 | 1 |
| | | 25.V.1947 | 1 |
| | Lido of Venice (San Nicolò) | V-1962 | 2 |
| | Lido of Venice (Alberoni) | 25.VI.1931 | 2 |
| | | 20.V.1944 | 1 |
| | | 1944-48 | 2 |
| | | 25.V.1945 | 3 |
| | | 8.VI.1947 | 10 |
| | | 4.VII.1949 | 1 |
| | | 30.V.1950 | 7 |
| | | 11.VI.1950 | 4 |
| | | 14.VII.1950 | 2 |
| | | 6.IX.1950 | 3 |
| | | 7.IX.1954 | 1 |
| | | 11.V.1955 | 3 |
| | | 29.VII.1958 | 1 |
| | | 6.V.1959 | 1 |
| | | 3-8.VI.1960 | 9 |
| | | 15.VI.1960 | 3 |
| | | 17.VI.1960 | 1 |
| | | 24.VI.1960 | 4 |
| | | 26.VIII.1960 | 1 |
| | | 28.VIII.1960 | 1 |
| | | 1.V.1961 | 2 |
| | | 2.V.1961 | 1 |
| | | 11.V.1961 | 2 |
| | | 5.VI.1961 | 3 |
| | | 20.VI.1961 | 1 |
| | | 9.VIII.1961 | 6 |
| | | 19.VIII.1961 | 2 |
| | | 15.VI.1962 | 6 |

continued

| Country (Region) | Locality | Date | Specimens |
|---------------------|------------------------------------|---------------|-----------|
| | | 19.VI.1962 | 5 |
| | | 2.VII.1962 | 15 |
| | | 2.VIII.1962 | 1 |
| | | 13.VIII.1962 | 2 |
| | | 23.V.1963 | 2 |
| | | 10.V.1965 | 7 |
| | | 15.III.1966 | 1 |
| | | 16-17.V.1966 | 9 |
| | | VI.1966 | 2 |
| | | 7-11.V.1967 | 3 |
| | | 18.V.1967 | 3 |
| | | 20.VI.1967 | 20 |
| | | 26.VI.1967 | 3 |
| | | 14.V.1968 | 1 |
| | | VI.1968 | 2 |
| | | 11-13.VI.1969 | 1 |
| | | VI.1969 | 3 |
| | | 6.III.1973 | 2 |
| | | 25.IV.2010 | 1 |
| | | 15.VIII.2012 | 1 |
| | | 10.IV.2014 | 3 |
| | | 6.V.2014 | 2 |
| | | 15.VII.2014 | 2 |
| | | 13.IV.2017 | 1 |
| | | 12.VI.2017 | 1 |
| | | 13.VII.2017 | 3 |
| | Sottomarina (VE) | 24.IV.1931 | 1 |
| | Ca' Roman (Pellestrina Island, VE) | 6.VI.1982 | 1 |
| | | 10.V.2006 | 1 |
| | | 10.VI.2006 | 1 |
| | Rosolina (RO) | 2.V.1962 | 1 |
| | | 4.VII.1962 | 5 |
| IT (Emilia Romagna) | Volano (FE) | 8-12.V.1972 | 1 |
| | | VI.1972 | 2 |
| no label | no label | no data | 2 |

Scarites terricola

| Country (Region) | Locality | Date | Specimens |
|----------------------------|---|---------------|-----------|
| IT (Friuli Venezia Giulia) | Lignano (UD) | 10.VII.1980 | 1 |
| IT (Veneto) | Lagoon of Venice (loc. Baccan) | 21.V.1986 | 4 |
| | Lagoon of Venice (Barena Ravaggio-3) | 14.IV.2010 | 1 |
| | Lagoon of Venice (Bonifica S. Leonardo) | 11.VI.1978 | 1 |
| | Lagoon of Venice (Cassa Colmata-A) | 8.VI.1975 | 4 |
| | | 3.VIII.1978 | 1 |
| | | 22.IV.1979 | 1 |
| | | 28.IV.1979 | 3 |
| | | 12.V.1979 | 1 |
| | | 18.V.1979 | 2 |
| | | 27.III.1991 | 1 |
| | Lagoon of Venice (Cassa Colmata-B) | 19.V.1979, | 1 |
| | | 2.VI.1979 | 1 |
| | | 22.VI.1979 | 1 |
| | | 7.VII.1979 | 5 |
| | | 27.VIII.1979 | 1 |
| | Lagoon of Venice (Cassa Colmata-DE) | 25.VI.1978 | 1 |
| | | 30.IX.1977 | 1 |
| | | 12.V.1987 | 7 |
| | Lagoon of Venice (Fusina) | 10.IX.1953 | 1 |
| | Lagoon of Venice (Marghera) | 5.V.1979 | 1 |
| | Lagoon of Venice (S. Elena) | 7.VI.1964 | 1 |
| | Lagoon of Venice (S. Erasmo) | 28.VI.1975 | 1 |
| | Lagoon of Venice (S. Giuliano) | 8.VI.1952 | 1 |
| | | 28.II.1954 | 1 |
| | Lagoon of Venice (Valle Averte) | 13.IX.1986 | 1 |
| | Lido of Venice (Alberoni) | 12.VI.2017 | 1 |
| | | 13.VII.2017 | 1 |
| | Punta Sabbioni (VE) | 25.IV.1952 | 1 |
| | | 17.VII.1955 | 1 |
| | | 31.VII.1955 | 1 |
| | | 19.VI.1955 | 1 |
| | | 5.VI.1956 | 3 |
| | | 31.III.1978 | 1 |
| | Jesolo Lido (VE) | VII.1962 | 1 |
| | | VII.1964 | 2 |
| | Porto Tolle (Sacca Scardovari; RO) | 19.VII.1993 | 1 |
| | | 22.VIII.1993 | 1 |
| | | 7.VI.1996 | 1 |
| | | 11.VI.1996 | 1 |
| | | 27.VI.1996 | 1 |
| | | 10-30.VI.1996 | 1 |
| IT (Emilia Romagna) | Volano (FE) | 30.VII.1971 | 1 |
| | | 8-12.V.1972 | 1 |
| IT (Sicily) | Gela (Biviere; CL) | 22.IV.1973 | 1 |
| | Vendicari (SR) | IV.1973 | 1 |
| IT (no data) | ex-coll. Ancilotto | no data | 1 |
| FR (Occitanie) | Ter a Perpignan | 30.V.1952 | 2 |