

Research Article

Integrative Taxonomy, Phylogeny, and New Species of the Weevil Genus *Onyxacalles* Stüben (Coleoptera: Curculionidae: Cryptorhynchinae)

Peter E. Stüben¹ and Jonas J. Astrin²

¹Curculio Institute, Hauweg 62, 41066 Mönchengladbach, Germany

²Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Molecular Taxonomy & Biobank, Adenauerallee 160, 53113 Bonn, Germany

Correspondence should be addressed to Peter E. Stüben, p.stueben@t-online.de

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A molecular phylogeny of the western Palearctic weevil genus *Onyxacalles* Stüben, 1999 is presented, combining two mitochondrial genes (COI and 16S) in a Bayesian analysis. Based on molecular data, *Onyxacalles pyrenaicus* Boheman, 1844 is transferred into the genus *Kyklioacalles* Stüben 1999 (*K. fausti* group) and—in an integrative taxonomy framework—the interaction between morphology and molecular analysis is illustrated. The species of *Onyxacalles* s. str. are assigned to three new species groups, *O. henoni*, *O. luigionii*, and *O. portusveneris* groups. The distribution of the related species in the Mediterranean area is illustrated with values of COI and 16S p-distances. Three new species are described and distinguished from their related species: *Onyxacalles nuraghi* Stüben sp.n. from Italy (Sardinia), *Onyxacalles torre* Stüben and Astrin sp. n. from France (Corsica) and *Onyxacalles vilae* Stüben sp. n. from Croatia (Velebit Mts.). A catalogue of all 20 species of *Onyxacalles* is given, and a key is finally presented combined with image stacking of the habitus and aedeagus for all species.

1. Introduction

Together with a number of other genera, the genus *Onyxacalles* Stüben, 1999 (Curculionidae: Cryptorhynchinae) was separated by Stüben [1] from the formerly excessively broadly circumscribed genus *Acalles* Schoenherr, 1825 as a group with initially 8 species. Since then, many new species of *Onyxacalles* have been described, mainly from Spain and North Africa. These discoveries were supported by the morphological finding that the three species from the Canary Islands belong to this genus [1, 2], a thesis that gained support from recent molecular analysis and has contributed to the new subgenus *Araneacalles* Stüben and Astrin [3]. This closed a “biogeographical gap” (between the Pyrenees and northwestern Africa) as a direct consequence of target-oriented collecting activities and descriptions of many new *Onyxacalles* species over the past decade [4–9]. Thus,

including the new species presented in this work, the genus now comprises 20 valid species.

Most species of *Onyxacalles* are found in the west Mediterranean area and on the Macaronesian Islands. Only one species, *Onyxacalles croaticus* (H. Brisout, 1897) [10], reaches Eastern Europe (Carpathians); another species, *O. amasyaensis* Wolf, 2001, was described from Turkey, but could be a synonym of *Onyxacalles denominandus* A. and F. Solari, 1907. This species richness in the west Mediterranean is well founded in the ecological preferences of *Onyxacalles*.

As “nocturnal goblins of the last primeval forests” [7], the species of *Onyxacalles* are not common in the often disturbed landscapes of the Iberian Peninsula and North Africa [11, 12]. These conditions provide good maps of relictual vegetation and information about the habitats, allowing us to trace these nocturnal Cryptorhynchinae in the dark and humid relicts of natural forests under big

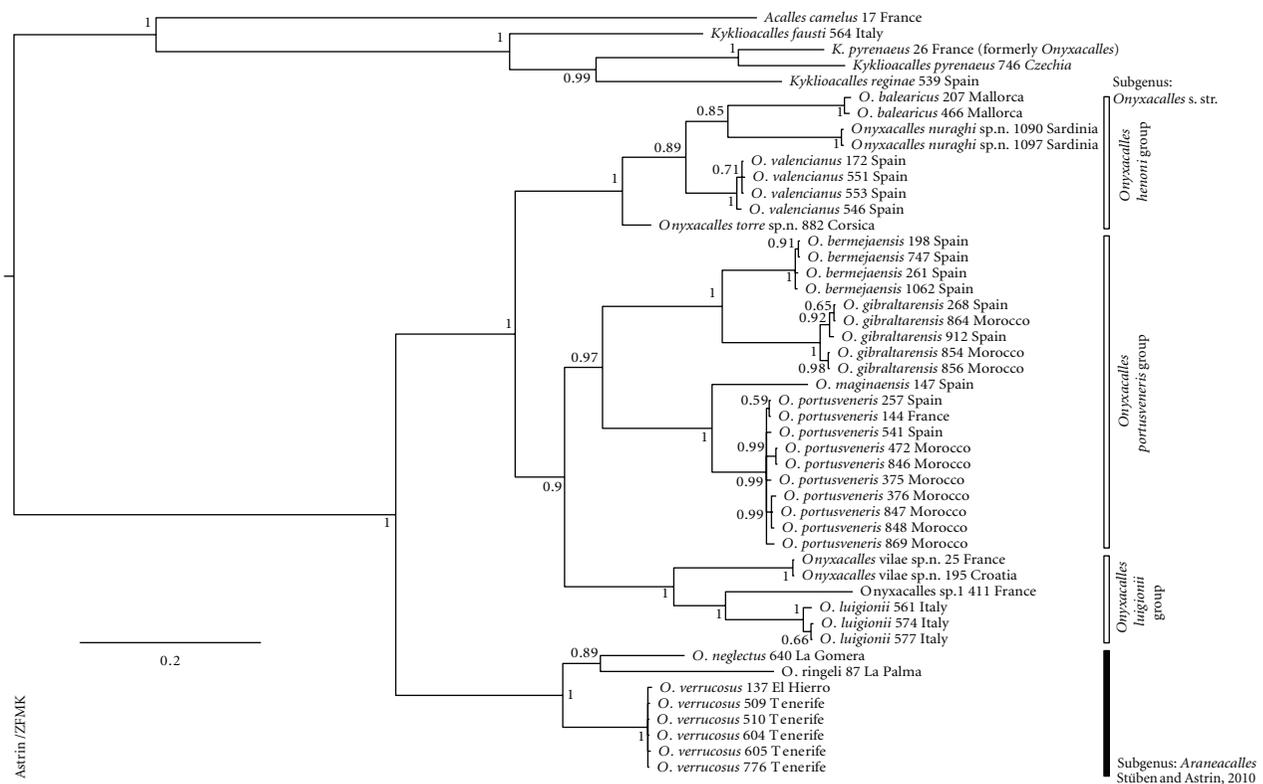


FIGURE 1: Bayesian consensus tree (50% majority rule) for COI and 16S.

oak trees and behind a dense jungle of *Smilax aspera* L. Therefore, sifting by day is not the ideal method of catching *Onyxacalles*. With their long legs, *Onyxacalles* species climb trees by night and were fogged by us from the canopy of the *laurisilva* on the Canary Islands of Tenerife and La Gomera [13, 14]. The flightless *Onyxacalles* are highly specialised woodlander inhabitant, and because of their restricted dispersal (above all on the European continent), they are an ideal bioindicator of original forest, highlighting that protection and sustainable development should concern us as entomologists and conservationists.

Moreover, with the study of the cryptic and similar *Onyxacalles* species, the taxonomist, especially the morphologist, enters a minefield. Due to intraspecific variability, the few external characteristics that are suitable for a differential diagnosis do not guarantee a reliable (re)identification of species: if the tufts of bristles exist or not, if the elytra are short oval or elongated, or if the midgroove of pronotum is more or less distinct—all these are important pointers, but are not conclusive. All *Onyxacalles* species have the hooked apex of the aedeagus in common, as the genus name implies (cf. Figures 9(a)–9(l)). However, a complex internal sac of the aedeagus (endophallus) does not exist—as it is typical for *Kyklioacalles*, *Dichromacalles*, or most genera from Macaronesia. Here, we are quickly stretched to our limits of a descriptive morphology.

With the “Molecular Weevil Identification” Project (see below), we tread a path towards an integrative taxonomy [15–21]. Molecular taxonomy is not only an addition or an

accessory “immunisation” to confirm morphological results. The integration of the two approaches must be done with the intention of *falsifying* and, if so, it can lead to a new way of viewing morphology: *interspecific* characteristics are discovered that are not regarded as belonging to *intraspecific* variability, or—more often—substituting the “human eyes,” the way we look at things. Instead of “anthropocentric conspicuities” (e.g., forms, colours, sizes), we focus on constitutive characteristics (e.g., apomorphies and homologies) that were previously overlooked in our diagnostic keys. An example is the latest history of the science behind the original species *Acalles pyrenaicus* Boheman, 1844 (see below).

Another telling example is the present classification of *Onyxacalles* s. str. into two species groups: the *O. luigionii*- and *O. pyrenaicus*-groups, based on the bristles of the elytral intervals (cf. [1, 8]). This hypothesis is no longer tenable, and this has nothing to do with superficial diagnosis of affinities or inaccurate observations. First, molecular analysis of related species reveals new informal species groups (see Figure 1) and makes evidence available to the morphologist, who then looks for new external characteristics. These are inconspicuous paradigm changes with a high impact [22], because the “puzzles,” in this case the *species*, which were previously pressurised within the framework of “normal science” (and more and more frequently caused difficulties) continue, but the emphasis of the characteristics under the new molecular phylogenetic paradigm has changed (see “Catalogue of *Onyxacalles*”), and new characteristics are discovered (see “Key to the species of *Onyxacalles*”).

The assumption that the morphologist should have seen a characteristic must be abandoned in favour of the question: would the morphologist be able to “see” it?

2. Catalogue of *Onyxacalles*

Species included in the molecular analysis are printed in bold (l.t. = type locality).

Genus: *Onyxacalles* Stüben, 1999a.

177 type species *Acalles luigionii* A. and F. Solari, 1907.

Subgenus: *Onyxacalles* s. str.

Onyxacalles henoni Group

balearicus Stüben, 2005: 115, Spain: Majorca (l.t.)

croaticus H. Brisout de Barneville, 1867: 62 (*Acalles*), Croatia (l.t.), Austria, Czech Republic, Germany, Poland, Slovakia, Slovenia

hannibali Germann, 2004: 118, Tunisia (l.t.)

henoni Bedel, 1888: 36 (*Acalles*), Algeria: Mt. Edough (l.t.).

nuraghi Stüben **sp. n.**, Italy: Sardinia (l.t.).

torre Stüben and Astrin **sp. n.**, France: Corsica (l.t.).

valencianus Germann, 2005: 104, Western Spain (l.t.).

Onyxacalles portusveneris Group

bermejaensis Stüben, 2001: 145, Spain (l.t.).

gibraltarensis Stüben, 2002: 206, Morocco (l.t.), Spain.

maginaensis Stüben, 2004: 120, Southern Spain (l.t.).

portusveneris Mayet, 1903: 74 (*Acalles*), France (l.t.), Spain, Morocco

seguraensis Stüben, 2003a: 201, Spain.

Onyxacalles luigionii Group

luigionii A. and F. Solari, 1907: 521 (*Acalles*), Central (l.t.) and Southern Italy.

vilae Stüben **sp. n.**, Croatia (l.t.), France: Isère (perhaps Austria and Slovenia).

cf. luigionii, France: Alpes Maritimes.

Incertae Sedis

denominandus A. and F. Solari, 1907: 523 (*Acalles*), Turkey (l.t.).

porcheti Hoffmann, 1935: 162 (*Acalles*), France: Pyrenees (probably a synonym of *A. luigionii*, see also Stüben 2007: 149).

amasyaensis Wolf, 2001: 150, Turkey (l.t.). (probably a synonym of *Acalles denominandus*)

Subgenus: *Araneacalles* Stüben and Astrin, 2010: 78 type species *Acalles verrucosus* Wollaston, 1863.

neglectus Kulbe, 1999: 193, Canary Islands: La Gomera (l.t.), El Hierro.

ringeli Kulbe 1999: 196, Canary Islands: La Palma (l.t.).

verrucosus Wollaston, 1863: 219 (*Acalles*), Canary Islands: Tenerife (l.t.), El Hierro.

3. Materials and Methods

The molecular analysis is based on 45 (43 after transfer of *O. pyrenaicus*, see below) individuals in 15 species or putative species of *Onyxacalles* and on 5 outgroup species (Cryptorhynchinae from 4 other genera; only the two closer genera are shown in the tree for better visualisation, while the 2 more distant ones were removed; see Table 1). Most sequences have been published in Astrin et al. (2012). Collecting and vouchering information as well as GenBank accession numbers are given in Table 1. Voucher specimens and extracted genomic DNA are deposited at the Biobank of the ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany).

DNA extraction was carried out on samples preserved in ethanol or on dried material, using Macherey-Nagel Nucleo Spin Tissue kits (Dueren, Germany) or BioSprint 96 kits (Qiagen, Hilden, Germany). We extracted DNA from either 2-3 legs, head and prothorax, or sometimes also the whole weevil, depending on size and conservation of the sample. PCR reaction mixes (50 μ L) contained 125 nmol MgCl₂, 5 μ L 10x PCR-buffer, 25 pmol of forward and reverse primer each, 5 pmol dNTPs, 1.75 units of *Taq* polymerase, and 5 μ L total undiluted DNA template. The lab chemicals were purchased from Sigma-Aldrich (Steinheim, Germany). We used the Qiagen (Hilden, Germany) Multiplex PCR kit in cases where the regular protocol failed. PCR primers were taken from Astrin and Stüben (2008; COI is based on the Folmer et al. [23] region; 16S is based on the Crandall and Fitzpatrick (1996) region). Primer sequences were as follows: LCOI490-JJ (COI forward, fw) 5'-CHACWAAYCATAAAGATATYGG-3', HCO2198-JJ (COI reverse, rev) 5'-AWACTTCVGGRTGVCCAAARAATCA-3'; 16S-ar-JJ (16S fw, erroneously as “rev” in [24]) 5'-CRCCTGTTTATTAACAT-3', 16S-1472-JJ (16S rev) 5'-AGATAGAAACCRACCTGG-3'. Thermal cycling was performed on blocks of the type GeneAmp PCR System 2700 (Applied Biosystems, Foster City, CA, USA). PCR program for 16S: first cycle set (15 repeats): 35 s denaturation at 94°C, 35 s annealing at 55°C (−1°C per cycle) and 60 s extension at 72°C. Second cycle set (25 repeats): 35 s denaturation at 94°C, 35 s annealing at 40°C, and 50 s extension at 72°C. PCR program for COI: same as for 16S, but annealing temperatures at 70°C and 55°C, with a decrease of 2°C per cycle in the first cycle set. Double-stranded sequencing was carried out by a sequencing facility (Macrogen, South Korea, and Netherlands) using the same primers as in PCR.

DNA sequence alignment was performed manually (COI) or using the MUSCLE ver. 3.6 programme [28] (16S), run with default parameters. Sequence length was 554 bp for 16S (aligned; longest sequence: 544 bp; shortest: 533 bp) and 658 bp for COI, for concatenated sequence data 1212 bp. The 16S alignment comprised 29 positions with

TABLE 1: Collecting data, vouchers, and GenBank accession numbers for the material analysed in this study. All specimens determined by P. E. Stüben, 2010 and 2011. Vouchers (DNA, morphology) are kept at the ZFMK Biobank. Most sequences have been published (or are reviewed) in Astrin et al. 2012 [21]. GenBank accession numbers of new sequences in this study start with "JN...". Taxonomic changes with regard to this publication are printed in brackets (old name).

| Taxon | Collecting data | DNA voucher | COI 16S |
|--|---|--|----------------------|
| <i>Acalles camelus</i> (Fabricius 1792) | France: Isère, 2 km SE Lans en Vercors, Montagne de Lans; N45°06'45" E05°36'21", 1352 m; Abies, Fagus, Fraxinus, 2005, Stüben | ZFMK-DNA-JJ0017, ZFMK-TIS-cl0026cam | EU286282 EU286447 |
| <i>Acallorneuma doderoi</i> A. and F. Solari 1908 | Italy: Sicilia (PA), 6 km SW Godrano, Bosco Ficuzza, Mte. Rocca Busambra; N37°51'38" E13°23'24", 1200 m; Quercus, Fraxinus, 2002, Stüben | ZFMK-DNA-JJ0065, ZFMK-TIS-cS0082dod | EU286292 EU286457 |
| <i>Cryptorhynchus lapathi</i> (Linné 1758) | Germany: Bienen bei Rees, Altrheinarm, 2004, Scharf | ZFMK-DNA-JJ0214, ZFMK-TIS-cD0354lap | EU286360 EU286523 |
| <i>Kyklioacalles fausti</i> (Meyer 1896) [25] | Italy: Campania, Cilento, 6 km SE Vallo d. Lucania, M. Sacro o Gelbison; N40°12'41" E15°19'42", 1544 m; Fagus, 2008, Stüben | ZFMK-DNA-JJ0564, ZFMK-TIS-cl625fau | GU213776 GU213772 |
| <i>Kyklioacalles pyrenaicus</i> (Boheman 1844) [26] (gen. <i>Onyxacalles</i>) | France: Isère, 14 km N Grenoble, Massif de la Chartreuse, NW Col de Porte; N45°18'40" E05°45'17", 1649 m; Abies, Fagus, Fraxinus, 2005, Stüben | ZFMK-DNA-JJ0026, ZFMK-TIS-cl0035pyr | GU988172 GU987762 |
| <i>Kyklioacalles pyrenaicus</i> [26] (gen. <i>Onyxacalles</i>) | Czech Republic: W Bohemia (KT), Balkovy, Doubrava Hill (6545), 2008, Kresl | ZFMK-DNA-JJ0764, ZFMK-TIS-cCz798pyr | GU981555 GU981506 |
| <i>Kyklioacalles reginae</i> Stüben 2003 | Spain: Teruel, S. Javalambre, Fuente la Risca near Arcos de las Salinas; N39°59'56" W01°01'21", 1121 m; Amelanchier ovalis, Acer monspessulanum, Erinacea anthyllis, Ulex, 2008, Stüben | ZFMK-DNA-JJ0539, ZFMK-TIS-cE600reg | GU981544 GU981495 |
| <i>Onyxacalles balearicus</i> Stüben 2005 | Spain: Mallorca, 3 km SE Lluc, Sra. de Tramuntana, Sa Maleta; N39°48'47" E02°53'23", 571 m; Quercus ilex, 2004, Stüben | ZFMK-DNA-JJ0207, ZFMK-TIS-cE0168bal | EU286357 EU286521 |
| <i>Onyxacalles balearicus</i> Stüben 2005 | Spain: Mallorca, 11 km NE Lluc, Sra. de Tramuntana; N39°52'03" E02°58'20", 107 m; PT, Smilax aspera, Quercus ilex, 2004, Stüben | ZFMK-DNA-JJ0466, ZFMK-TIS-cE0294bal | GU988348 ----- |
| <i>Onyxacalles bermejaensis</i> Stüben 2001 | Spain: Andalucía, 11 km S Ronda, Sierra de las Nieves; N36°39'51" W05°05'01", 1047 m; Quercus ilex, 2005, Stüben | ZFMK-DNA-JJ0198, ZFMK-TIS-cE0167ber | EU286350 EU286514 |
| <i>Onyxacalles bermejaensis</i> Stüben 2001 | Spain: Málaga, 9 km SE Ubrique, Sierra de Líbar; N36°36'52" W05°23'16", 663 m; Quercus ilex, Ceratonia, 2007, Stüben | ZFMK-DNA-JJ0261, ZFMK-TIS-cE0194ber | GU988244 GU987827 |
| <i>Onyxacalles bermejaensis</i> Stüben 2001 | Spain: Málaga, NW Marbella, Sierra de las Nieves; N36°39'52" W05°04'57", 1043 m; Quercus ilex, Echinodera spinosa, 2009, Stüben | ZFMK-DNA-JJ0747, ZFMK-TIS-cE778ber | GU988506 GU988066 |
| <i>Onyxacalles bermejaensis</i> Stüben 2001 | Spain: Prov. Málaga, Algatocín, near Opayar; N36°34'39" W05°18'13", 576 m, Quercus sp., 17.8.2010, Stüben | ZFMK-DNA-JJ1062, ZFMK-TIS-cES1062 | JN121398 ----- |
| <i>Onyxacalles gibraltarensis</i> Stüben 2002 | Spain: Cádiz, 10 km SW Algeciras, El Bujeo; N36°04'10" W05°31'48", 257 m; Quercus suber, 2007, Stüben | ZFMK-DNA-JJ0268, ZFMK-TIS-cE0206gib | GU988249 GU987832 |
| <i>Onyxacalles gibraltarensis</i> Stüben 2002 | Morocco: Rif, SW Oued-Laou, river, O. Laou; N35°17'47" W05°13'38", 210 m; Quercus suber, Smilax, Arbutus, 2009, Stüben | ZFMK-DNA-JJ0854, ZFMK-TIS-cE897gib | GU988577 GU988137 |
| <i>Onyxacalles gibraltarensis</i> Stüben 2002 | Morocco: W Sebta, vir. Biutz; N35°53'04" W05°24'08", 337 m; Quercus suber, Smilax, Arbutus, 2009, Stüben | ZFMK-DNA-JJ0856, ZFMK-TIS-cE899gib | GU988578 GU988138 |
| <i>Onyxacalles gibraltarensis</i> Stüben 2002 | Morocco: S Ksar-es-Seghir; N35°45'16" W05°30'49", 278 m; Pistacia, Quercus suber, 2009, Stüben | ZFMK-DNA-JJ0864, ZFMK-TIS-cE907gib | GU988584 GU988144 |
| <i>Onyxacalles gibraltarensis</i> Stüben 2002 | Spain: Cádiz, Los Barrios, Alcornocales N.P., between Facinos, Río Las Cañas and Mantera Torero; Olea europaea, 2009, Torres | ZFMK-DNA-JJ0912, ZFMK-TIS-cE949gib | GU988608 ----- |
| <i>Onyxacalles luigionii</i> (A. & F. Solari 1907) | Italy: Campania, Cilento, 6 km SE Vallo d. Lucania, M. Sacro o Gelbison; N40°12'41" E15°19'42", 1544 m; Fagus, 2008, Stüben | ZFMK-DNA-JJ0561, ZFMK-TIS-cl622lui | GU988407 GU987967 |

TABLE 1: Continued.

| Taxon | Collecting data | DNA voucher | COI 16S |
|--|---|--|-------------------------|
| <i>Onyxacalles luigionii</i> (A. & F. Solari 1907) | Italy: Campania, Monti Picentini, 9 km N Acerno, Piano Laceno; N40° 48' 58'' E15° 07' 35'', 1210 m; Fagus, 2008, Stüben | ZFMK-DNA-JJ0574, ZFMK-TIS-cl635lui | GU988417 GU987977 |
| <i>Onyxacalles luigionii</i> (A. & F. Solari 1907) | Italy: Basilicata, Monte Pollino, 9 km SE Rotonda, Rif. de Gasperi; N39° 54' 37'' E16° 07' 15'', 1486 m; Fagus, 2008, Stüben | ZFMK-DNA-JJ0577, ZFMK-TIS-cl638lui | GU988418 GU987979 |
| <i>Onyxacalles maginaensis</i> Stüben 2004 | Spain: Andalucía, 28 km E Jaén, Sierra Magina; N37° 43' 21'' W03° 29' 11'', 1600 m; Quercus ilex, 2005, Stüben | ZFMK-DNA-JJ0147, ZFMK-TIS-cE0169mag | EU286327 EU286491 |
| <i>Onyxacalles maginaensis</i> Stüben 2004 | Spain: Almería, 11 km NW Laujar de Andarax, Sierra Nevada, Bayárcal; N37° 02' 27'' W03° 00' 12'', 1291 m; Quercus ilex, 2007, Stüben | ZFMK-DNA-JJ0257, ZFMK-TIS-cE0187mag | submitted to GenBank |
| <i>Onyxacalles maginaensis</i> Stüben 2004 | Spain: Teruel, S. Javalambre, Fuente la Risca near Arcos de las Salinas; N39° 59' 56'' W01° 01' 21'', 1121 m; Amelanchier ovalis, Acer monspessulanum, Erinacea anthyllis, Ulex, 2008, Stüben | ZFMK-DNA-JJ0541, ZFMK-TIS-cE602mag | GU988390 GU987950 |
| <i>Onyxacalles neglectus</i> Kulbe 1999 | Spain: Canary Islands, La Gomera, S Hermigua, El Cedro, Las Mimbreras; N28° 07' 27'' W17° 13' 26'', 901 m; laurisilva, 2008, Astrin and Stüben | ZFMK-DNA-JJ0640, ZFMK-TIS-cE713neg | FJ716525 GU988014 |
| <i>Onyxacalles nuraghi</i> sp.n. | Italy: W-Sardinia, E Macomer: above Lei; N40° 19' 54'' E08° 53' 49'', 1020 m; Quercus, Acer monspessulanum, 4.10.2010, Stüben | ZFMK-DNA-JJ1090, ZFMK-TIS-cIT1090 | JN642097 JN121399 |
| <i>Onyxacalles nuraghi</i> sp.n. | Italy: W-Sardinia, E Macomer: above Lei; N40° 19' 17'' E08° 53' 52'', 586 m; Quercus ilex, 7.10.2010, Stüben | ZFMK-DNA-JJ1097, ZFMK-TIS-cIT1097 | JN642098 JN121300 |
| <i>Onyxacalles portusveneris</i> (Mayet 1903) [27] | France: Gard, 15 km NE Nimes, Pont du Gard, Collias; N43° 57' 03'' E04° 28' 59'', 68 m; Quercus ilex, 2006, Stüben | ZFMK-DNA-JJ0144, ZFMK-TIS-cF0166por | EU286326 EU286490 |
| <i>Onyxacalles portusveneris</i> (Mayet 1903) [27] | Morocco: Rif Mts., 10 km W Ketama = Issague; N34° 57' 40'' W04° 40' 51'', 1600 m; Prunus lusitanica, 2001, Stüben | ZFMK-DNA-JJ0375, ZFMK-TIS-cM480por | GU988311 ----- |
| <i>Onyxacalles portusveneris</i> (Mayet 1903) [27] | Morocco: M-Atlas, 10 km S Ain-Leuh; N33° 13' 48'' W05° 20' 50'', 1700 m; Quercus ilex, Rubus, Cedrus, 2002, Stüben | ZFMK-DNA-JJ0376, ZFMK-TIS-cM481por | GU988312 ----- |
| <i>Onyxacalles portusveneris</i> (Mayet 1903) [27] | Morocco: High Atlas, E Marrakech, N Taddert, (near Tazouguerte); N31° 28' 07'' W07° 24' 59'', 1727 m; Quercus, 2009, Stüben | ZFMK-DNA-JJ0846, ZFMK-TIS-cE889port | GU988573 GU988133 |
| <i>Onyxacalles portusveneris</i> (Mayet 1903) [27] | Morocco: Middle Atlas, S Azrou, Äin Leuh; N33° 16' 50'' W05° 20' 18'', 1582 m; Quercus ilex, Euphorbia, 2009, Stüben | ZFMK-DNA-JJ0847, ZFMK-TIS-cE890port | GU988574 GU988134 |
| <i>Onyxacalles portusveneris</i> (Mayet 1903) [27] | Morocco: Middle Atlas, S Azrou, S Äin Leuh; N33° 14' 57'' W05° 21' 04'', 1715 m; Quercus ilex, 2009, Stüben | ZFMK-DNA-JJ0848, ZFMK-TIS-cE891port | GU988575 GU988135 |
| <i>Onyxacalles portusveneris</i> (Mayet 1903) [27] | Morocco: Rif, 10 km W Ketama; N34° 57' 40'' W04° 40' 51'', 1600 m; Cedrus, Prunus, 2009, Stüben | ZFMK-DNA-JJ0869, ZFMK-TIS-cE912port | GU988587 GU988147 |
| <i>Onyxacalles portusveneris</i> (Mayet 1903) [27] (<i>Onyxacalles</i> sp.) | Morocco: High Atlas, 59 km SE Marrakech; N31° 28' 19'' W07° 24' 22'', 1500 m; Quercus ilex, Quercus suber, 2002, Stüben | ZFMK-DNA-JJ0472, ZFMK-TIS-cM482mag | GU988350 GU987922 |
| <i>Onyxacalles ringeli</i> Kulbe 1999 | Spain: Canary Islands, La Palma, Cumbre Nueva, 4,5 km SE El Paso, El Pilar; N28° 37' 37'' W17° 49' 45'', 1432 m; laurisilva, 2006, Stüben | ZFMK-DNA-JJ0087, ZFMK-TIS-cC0171rin | EU286300 EU286465 |
| <i>Onyxacalles</i> sp. 1 (<i>O. luigionii</i>) | France: Alpes-Maritimes, 3 km W Sospel, Col de Braus; N43° 52' 34'' E07° 24' 17'', 1051 m; Quercus pubescens, Ostrya carpinifolia, broom, 2007, Stüben | ZFMK-DNA-JJ0411, ZFMK-TIS-cF440lui | GU988325 GU987897 |
| <i>Onyxacalles torre</i> sp. n. (<i>O. henoni</i>) | France: Corsica, Col de Vizzavona, 22 km S Corte; N42° 06' 45'' E09° 06' 49'', 1100 m; Fagus, 2001, Stüben | ZFMK-DNA-JJ0882, ZFMK-TIS-cF479hen | GU988592 ----- |

TABLE 1: Continued.

| Taxon | Collecting data | DNA voucher | COI 16S |
|---|---|---|----------------------|
| <i>Onyxacalles valencianus</i> Germann 2005 | Spain: Alicante, 7 km SW Alcoi, Sierra de Menechaor, Santurio de la Font Roja; N38°39'34'' W00°32'29'', 1296 m; Quercus ilex, 2007, Stüben | ZFMK-DNA-JJ0172, ZFMK-TIS-cE0180val | EU286331 EU286495 |
| <i>Onyxacalles valencianus</i> Germann 2005 | Spain: Castellón, Morella, Barranco de la Bota; N40°33'12'' W00°00'27'', 814 m; Quercus ilex, Hedera helix, 2008, Stüben | ZFMK-DNA-JJ0546, ZFMK-TIS-cE607val | GU988393 GU987953 |
| <i>Onyxacalles valencianus</i> Germann 2005 | Spain: Barcelona, above dry river bed, near Vallirana; N41°22'36'' E01°55'02'', 245 m; Quercus ilex, Ficus carica, Smilax aspera, 2008, Stüben | ZFMK-DNA-JJ0551, ZFMK-TIS-cE612val | GU988398 GU987958 |
| <i>Onyxacalles valencianus</i> Germann 2005 | Spain: Barcelona, S. Montseny, Tordera valley, near St. Marçal; N41°48'01'' E02°25'15'', 1060 m, 2008, Stüben | ZFMK-DNA-JJ0553, ZFMK-TIS-cE614val | GU988400 GU987960 |
| <i>Onyxacalles verrucosus</i> (Wollaston 1863) | Spain: Canary Islands, El Hierro, 7 km W La Frontera, Pista Derrabado; N27°44'29'' W18°03'24'', 895 m; Laurus azorica, 2006, Stüben | ZFMK-DNA-JJ0137, ZFMK-TIS-cC0170ver | EU286324 EU286488 |
| <i>Onyxacalles verrucosus</i> (Wollaston 1863) | Spain: Canary Islands, Tenerife, 6 km N La Laguna, Monte de las Mercedes; N28°31'50'' W16°17'09'', 950 m; laurisilva, 2003, Stüben | ZFMK-DNA-JJ0509, ZFMK-TIS-cE570ver | ----- GU987937 |
| <i>Onyxacalles verrucosus</i> (Wollaston 1863) | Spain: Canary Islands, Tenerife, 4 km S Los Silos, Teno Mts., Monte del Agua; N28°19'20'' W16°49'14'', 700 m; laurisilva, 2003, Stüben | ZFMK-DNA-JJ0510, ZFMK-TIS-cE571ver | GU988373 GU987938 |
| <i>Onyxacalles verrucosus</i> (Wollaston 1863) | Spain: Canary Islands, Tenerife, NE La Laguna, Anaga Mts. near Moquinal; N28°31'55'' W16°17'24'', 840 m; laurisilva, 2008, Astrin and Stüben | ZFMK-DNA-JJ0604, ZFMK-TIS-cE677ver | GU988433 GU987995 |
| <i>Onyxacalles verrucosus</i> (Wollaston 1863) | Spain: Canary Islands, Tenerife, NE La Laguna, Anaga Mts. near Chinobre; N28°33'21'' W16°10'46'', 808 m; Laurus, Ixanthus viscosus, 2008, Astrin and Stüben | ZFMK-DNA-JJ0605, ZFMK-TIS-cE678ver | GU988434 GU987996 |
| <i>Onyxacalles verrucosus</i> (Wollaston 1863) | Spain: Canary Islands, Tenerife, SW Los Silos, Teno Mts., Monte del Agua, Chupadero; N28°19'23'' W16°49'12'', 940 m; Laurus novocanariensis, 2008, Astrin, Stüben, Behne and Floren | ZFMK-DNA-JJ0776, ZFMK-TIS-cE813ver | GU988524 GU988085 |
| <i>Onyxacalles vilae</i> sp.n. (<i>O. luigionii</i>) | France: Isère, 2 km SE Lans en Vercors, Montagne de Lans; N45°06'45'' E05°36'21'', 1352 m; Abies, Fagus, Fraxinus, 2005, Stüben | ZFMK-DNA-JJ0025, ZFMK-TIS-cI0027lui | EU286286 EU286451 |
| <i>Onyxacalles vilae</i> sp.n. (<i>O. luigionii</i>) | Croatia: Dalmatian, 8 km E Karlobag, Velebit Mts., Stupacinovo; N44°32'41'' E15°09'58'', 1049 m; Fagus, 2007, Stüben | ZFMK-DNA-JJ0195, ZFMK-TIS-cHR0339lui | EU286348 EU286512 |

gaps. All of these were included into phylogenetic analysis. We implemented the GTR+I+ Γ [29] model of nucleotide substitution for both genes in Bayesian MCMC analyses, run in MrBayes ver. 3.1.2 [30]. Only COI was included for the new sequences. We ran two independent replicates for 10 million generations per analysis (each with 1 cold chain and 3 chains of different temperature). Every 1'000th tree was sampled (20'000 trees retained). Negative log-likelihood score stabilisation was determined in a separate visualisation (in MS Excel). Accordingly, we retained 19.800 trees (after discarding burn-in), of which a 50%-majority rule consensus tree was built, with posterior probabilities (Figure 1).

4. Results and Discussion

4.1. A Gestalt Switch—Changing the Way You See: *Kyklioacalles pyrenaicus* (Boheman, 1844). The species of *Onyxacalles* are characterised by a particularly long and slender rostrum which is at least 3-4 times as long as wide between the

insertions of the antennae. A further conspicuous feature (not typical for western Palearctic Cryptorhynchinae—excepting the species of the Macaronesian Islands) is the unusually long and slender (arachnoid) legs. The name of this genus refers to the hook-shaped tip of the aedeagus. No further species of the former accumulative genus *Acalles* or of other western Palearctic genera of the Cryptorhynchinae exhibit such a characteristic hook-shaped tip of the aedeagus (*onyx*; greek: hook, hook-shaped tool). Complex-sclerotised structures of the internal sac are absent or reduced to simple line- or bar-like structures. These structures have been significant, for instance, for the partly phylogeny-based classification and determination of the genera and species of *Dichromacalles* and *Kyklioacalles*. The strongly sclerotised median lobe exhibits either only unclear structures or none at all (see [31]).

As early as the beginning of the last century, in their ground-breaking revision of the western Palearctic species of *Acalles* s.l., A. and F. Solari placed the species *A. pyrenaicus*

Boheman, 1844, *A. henoni* Bedel, 1888, *A. croaticus* Brisout, 1867, and *A. luigionii* Solari, 1907—although together with further species—into the same group (see IV. group; [32]). Together with initially 7 further species (among it the above species denominated by A. and F. Solari, as well as 3 further species from the Canary Islands), they were transferred into the new genus *Onyxacalles* [1, page 186], a genus that currently comprises 20 species.

However, *Onyxacalles pyrenaicus* is a polymorphic species, with regard to the outline of the aedeagus as well as the more or less ovals rounded elytra [1, page 188]. This is—among others—the reason why we could not ascertain definitively whether the subspecies *Acalles pyrenaicus germanicus* Letzner, 1882 (= *Onyxacalles boehmei* Košťál & Holecová, 2001 [33] syn.) is really a junior synonym or not (even if the first author considers it a synonym; cf. [7, page 123]).

In addition to *Onyxacalles portusveneris* (Mayet, 1903) (see Figure 4), *O. pyrenaicus* has an exceptionally large distribution area (cf. [31]). This could explain the high genetic distances of the mitochondrial COI and 16S gene (e.g., France: Lans en Vercors—Austria: Merkersdorf, p-distances: COI = 8,5%, 16S = 2,4%). This species can be found from the Pyrenees to the mountains of Western, Central, and Eastern Europe to the Carpathians and can be beaten from the branches of different conifers, especially larch, but can also be sifted under deciduous trees (e.g., *Fagus*).

This does not coincide with the other *Onyxacalles* species, which live on different deciduous trees and never prefer conifers. Apart from these ecological conditions, we can establish that the above-mentioned differences to the other genera of the western Palearctic Cryptorhynchinae point to a closer relationship to the species of *Onyxacalles*, a view with which most authors concur (e.g., [33]).

In any case, the taxonomists did not pay attention to the distinct ecology and—in comparison with the other species of *Onyxacalles*—the clearly narrower aedeagus (cf. Figure 6(k) versus Figures 9(a)–9(l)). Are these peripheral characteristics? And in which genus of Cryptorhynchinae is it possible to place this species (without the need for a monotypic genus)? The first author had never imagined assigning this species to the genus *Kykliaocalles* Stüben, 1999. There was no reason for such a review, not even an “initial suspicion” (see below).

However, this presumed “*Onyxacalles*” species appears deeply nested within the genus *Kykliaocalles* in the dendrogram [34, Figure 1]. This inclusion within *Kykliaocalles* is maximally supported. Furthermore, it is obvious that *Acalles pyrenaicus* forms a clade with *K. fausti* (Meyer, 1896), *K. reginae* Stüben, 2003, *K. saccoi* (Colonnelli, 1973) [35], and *K. reinosae* (H. Brisout de Barneville, 1867) [10, 34]. Two species, *K. reginae* and *K. reinosae*, are distinguished from the other species by the completely different habitus, but chiefly belong and were allocated early on to the *K. fausti* group “only” on the basis of the endophallus. This allocation has been shown to be justified by molecular data [34].

But what would have happened if *Kykliaocalles* had not been defined initially on the basis of the cyclical structure of the endophallus, as the name implies [36], and as an

immediate consequence, *Acalles pyrenaicus* would not have been eliminated? Putting it the other way round: what if the similarity between this species *Kykliaocalles saccoi* and *Kykliaocalles fausti* had been considered in a habitus-to-habitus comparison? That is not only a simple, retrospective, and dispensable “what-if” question, because in this case one brings the fact to mind that *A. pyrenaicus* must now be coercively placed among the *Kykliaocalles* species, Figures 8(f)–8(h).

The definition especially of a higher taxon is an arbitrary supposition. As taxonomists we always operate with *constructs* and as morphologists we *find* characteristics that are prominent to our eyes (and sometimes “we like to see”). It must be admitted that extremely rarely do we look for homologies, which in theory constitute the best criterion (e.g., [37]), but are in practice often difficult to find when dealing with cryptic and similar-looking species.

This change of mind and perception is similar to a Gestalt switch [22], a figure spinning in two directions: the contour line of the species is the same, but the species is not (as in the Gestalt psychology, the vase-face and duck-rabbit illusions). We cannot explain this Gestalt switch based on morphological research alone, and we cannot build and establish it *within* this framework. But we know the cause for this inconspicuous paradigm change: only extrinsic evidence from DNA analysis has *opened* the morphologist’s eyes in this case—and this in the true sense of the word.

4.2. Integrative Taxonomy: Changing the Way You Look for Species. Integrative taxonomy sounds like an accumulation of different disciplines: morphology, molecular biology, ecology, ethology, and biogeography deliver the ingredients. But this is not invariably the case, and not so simple. It is a more eventful, reciprocal exchange of *evidence*, which an initial suspicion either confirms or rejects (comparable to an unsolved criminal case).

An initial morphological suspicion was already available when we discovered the new species *Onyxacalles nuraghi* (*O. henoni* group) in the humid *Quercus/Acer* forest in the mountains of Marghine on Sardinia. The differences from the well-known species of this group are obvious and easy to assemble (see below differential diagnosis of *O. nuraghi*). In the case of *Onyxacalles vilae* sp. n. (*O. luigionii* group) from the Velebit Mountains (Croatia), it was morphologically more ambiguous, but in case of the third species *Onyxacalles torre* sp.n. (*O. henoni* group) from Corsica, the specimens of the current type series remained completely unnoticed in the collection for years.

But the molecular results in view of these three (resp. four) species are obvious (see also Figures 1–4). With maximal support, *O. vilae* is widely separated in the tree topology from *O. nuraghi* and *O. torre* (*O. henoni* group; Figure 1). Together with *Onyxacalles* sp. 1, *O. vilae* groups with *O. luigionii* (*Onyxacalles* sp. 1 as sister taxon of the latter), but all these species are separated by considerable p-distances (>9% COI and >4% 16S; Figure 3). Interestingly, the *O. vilae* specimen from Croatia shares the haplotype of the French specimen. *O. torre* and *O. nuraghi* are genetically closer to each other (1,8% 16S; Figure 2), but not sister species.

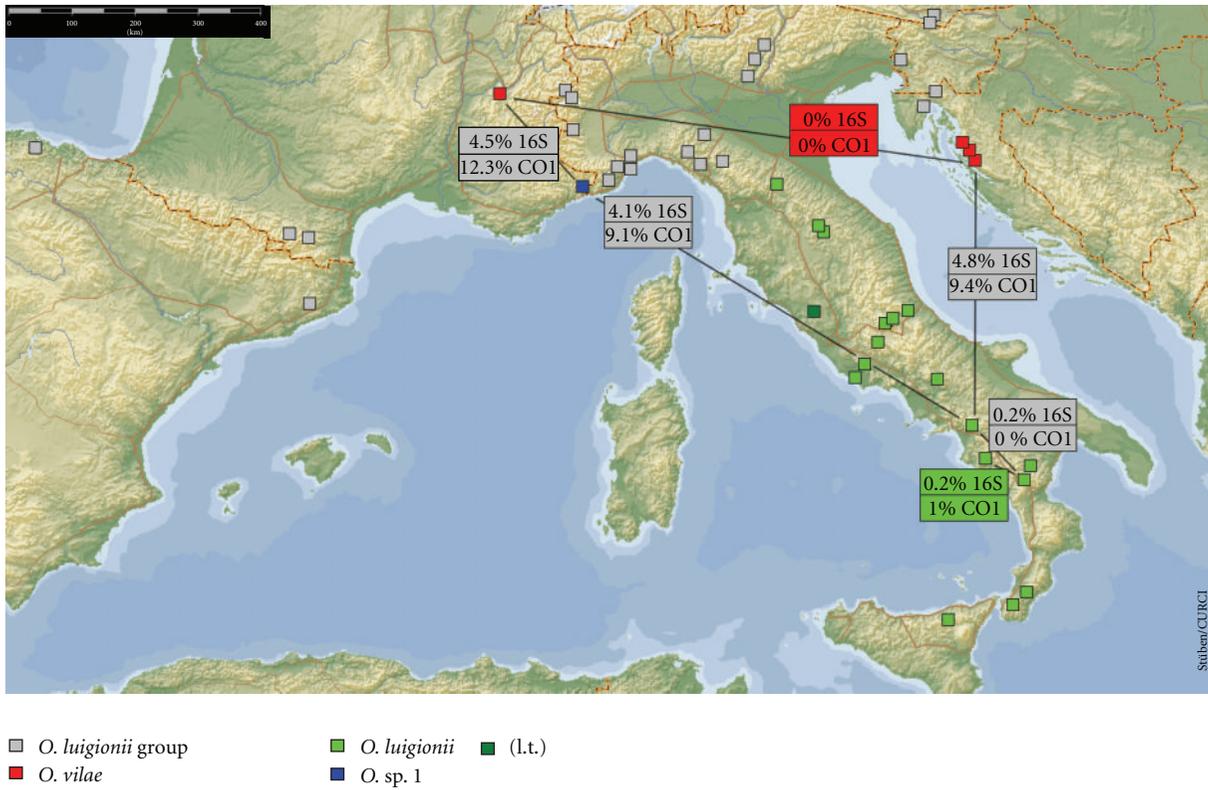


FIGURE 3: Distribution of related species of the *O. luigionii* group in the Mediterranean area with values of COI and 16S p-distances.

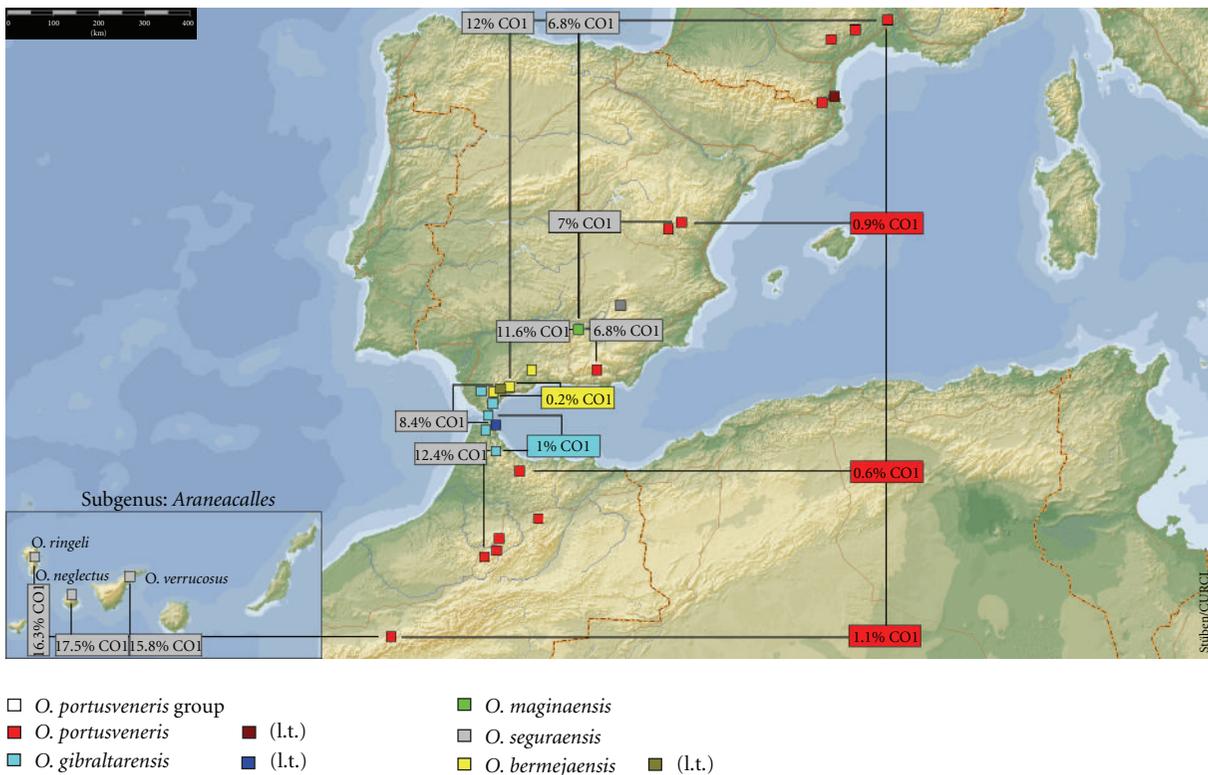


FIGURE 4: Distribution of related species of the *O. portusveneris* group in the Mediterranean area with values of COI p-distance (658 bp).

Genus: *Onyxacalles* Stüben, 1999, Type species: *Acalles luigonii* A. and F. Solari, 1907 (L.t.: Central Italy).

5.1. New Species of the *Onyxacalles henoni* Group

5.1.1. *Onyxacalles nuraghi* Stüben sp. n.

(Figures 5(a)–5(c), 5(i), 6(l)).

Type Material

Holotype (1♂). Italy: Sardinia, Macomer, Lei, N40°19'54'' E08°53'49'', 1020 m, *Quercus*, *Acer monspesulanus*, 4.10.2010, leg. Stüben-27-, coll. CURCULIO-Institut, D-Mönchengladbach.

Paratypes (1♂). Data as for holotype, coll. Stüben; 4♂, 1♀: Italy: Sardinia, Macomer, Lei, N40°19'17'' E08°53'52'', 586 m, *Quercus ilex*, 7.10.2010, leg. Stüben-33-, coll. Stüben, CURCULIO-Institut, D-Mönchengladbach (1♀), coll ZFMK, 1♂: ZFMK-DNA-JJ1097, ZFMK-TIS-cIT1097.

DNATYPE (1♂). Data as for holotype, coll. ZFMK: ZFMK-DNA-JJ1090, ZFMK-TIS-cIT1090; GenBank Acc. no COI: JN121399, 16S: JN642097.

Differential Diagnosis. The new species from the south-facing slope of the Chain of Marghine (Italy: Sardinia) belongs—from a morphological and molecular perspective—to the *Onyxacalles henoni* group and should be compared with the most closely related species from Majorca (Spain): *Onyxacalles balearicus* Stüben, 2005.

Onyxacalles nuraghi

- (1) Disc of pronotum with a channel from the base towards the flat sector in front of the fore-margin; with tufts of bristles on both sides of the channel (Figure 5(i)).
- (2) Bristles on the elytral intervals at least 2x as long as wide; shaping tufts with big gaps; their distances range from 3x the length of bristles.
- (3) Elytra of male with parallel sides in the middle sector (dorsal view); contour line of elytra forms almost a semicircle in lateral view (Figure 5(a)).
- (4) Apex (“hook”) of the aedeagus (in ventral view) smaller (Figure 5(c)).

Onyxacalles balearicus

- (1*) Disc of pronotum without a channel and without tufts of bristles (Figure 5(h)).
- (2*) The free-standing bristles on the intervals shorter, 1.3x as long as wide; placed in a single row, not forming tufts.
- (3*) Elytra of male broader and stronger (short ovaly) rounded (slightly “egg shaped”); contour line of

elytra flatter or slightly rounded behind the base in lateral view (Figure 5(g)).

- (4*) Apex (hook) of the aedeagus (in ventral view) broader (Figure 5(j)).

The new species from Sardinia is different from *Onyxacalles henoni* (Bedel, 1888) [38] (Algeria: Mt. Edough, *loc. typ.*), with which it has the tufts of bristles on the elytral intervals in common, by (1) darker elytral integument (Figure 5(a) versus 5(k)), (2) finer and longer white bristles on the femora, and (3) longer apex (“hook”) of the aedeagus (lateral view, see Figure 5(c) versus 5(n)). It can be distinguished from *Onyxacalles valencianus* Germann, 2005 from the Spanish mainland (Barcelona: Villarana, *loc. typ.*) by (1) elytral tufts of bristles (versus single bristles), (2) deep channel of the pronotum (versus without channel), and (3) longer apex of aedeagus (lateral view, see Figure 5(c) versus 9(h)).

For a comparison with all other species see below the “Key to the species, of *Onyxacalles* Stüben, 1999”.

Description

Length. 2.60–3.40 mm (without rostrum).

Head and Rostrum. Eyes large; rounded ovally towards front and acuminate towards underside of rostrum; frons between eyes more slender than the base of rostrum; rostrum reddish brown, closely covered with white scales at the base; rostrum of male reaching 3/4 length of pronotum and finely punctuated towards apex; rostrum of females reaching 4/5 length of pronotum, slender, shiny, and even more finely punctuated. The last three funicles of antennae short ovaly rounded; the first two funicles elongated; the club clearly separated from funicles.

Pronotum. Widest at the end of the first third of the pronotum (holotype: 1.17x as wide as long); well rounded laterally towards the fore-margin and the base; with a deep depression at the sides directly behind the fore-margin; disk of pronotum strongly arched, with a channel in the middle from the base towards the flat sector in front of the fore-margin. The integument is rich in contrast consisting of round black scales on the disk and oval, white/brown scales on the flanks of the pronotum. Elongated and black bristles in an upright position in the middle of the disk on both sides of the channel; with a similar, but white tuft of bristles on each side of the pronotum; the deep punctures always covered with scales.

Elytra. Oblong (holotype: 1.29x as long as wide); widest in the middle and there with nearly parallel sides; only slightly rounded directly in front of the base; short ovaly rounded towards the apex. Contour line of elytra strongly arched, almost forming a semi circle. The shiny and predominantly dark brown integument with a beige/white crescent-shaped fascia in front of the base and on the elytral slope. Bristles on the first and third interval (excluding the suture stripe)

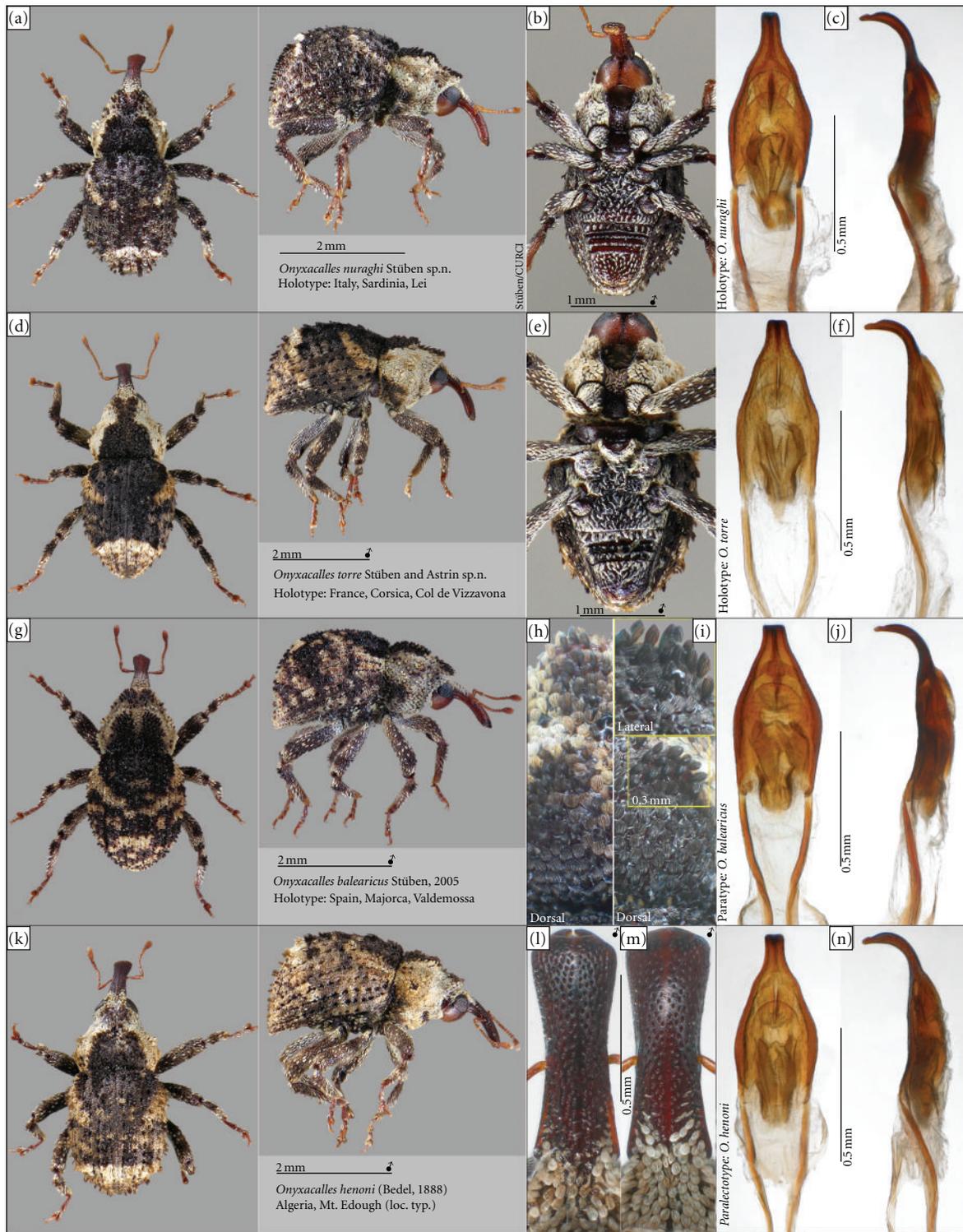


FIGURE 5: (a)–(c) *O. nuraghi* sp.n.—habitus (dor./lat./ven.), aedeagus (ven./lat.). (d–f) *O. torre* sp. n.—habitus (dor./lat./ven.), aedeagus (ven./lat.); (g, j) *O. balearicus*—habitus (dor./lat.), aedeagus (ven./lat.); (k, n) *O. henoni*—habitus (dor./lat.), aedeagus (ven./lat.). By comparison, bristle of pronotum—*O. balearicus* (h) versus *O. nuraghi* (i); rostrum—*O. henoni* (l) versus *O. torre* (m).

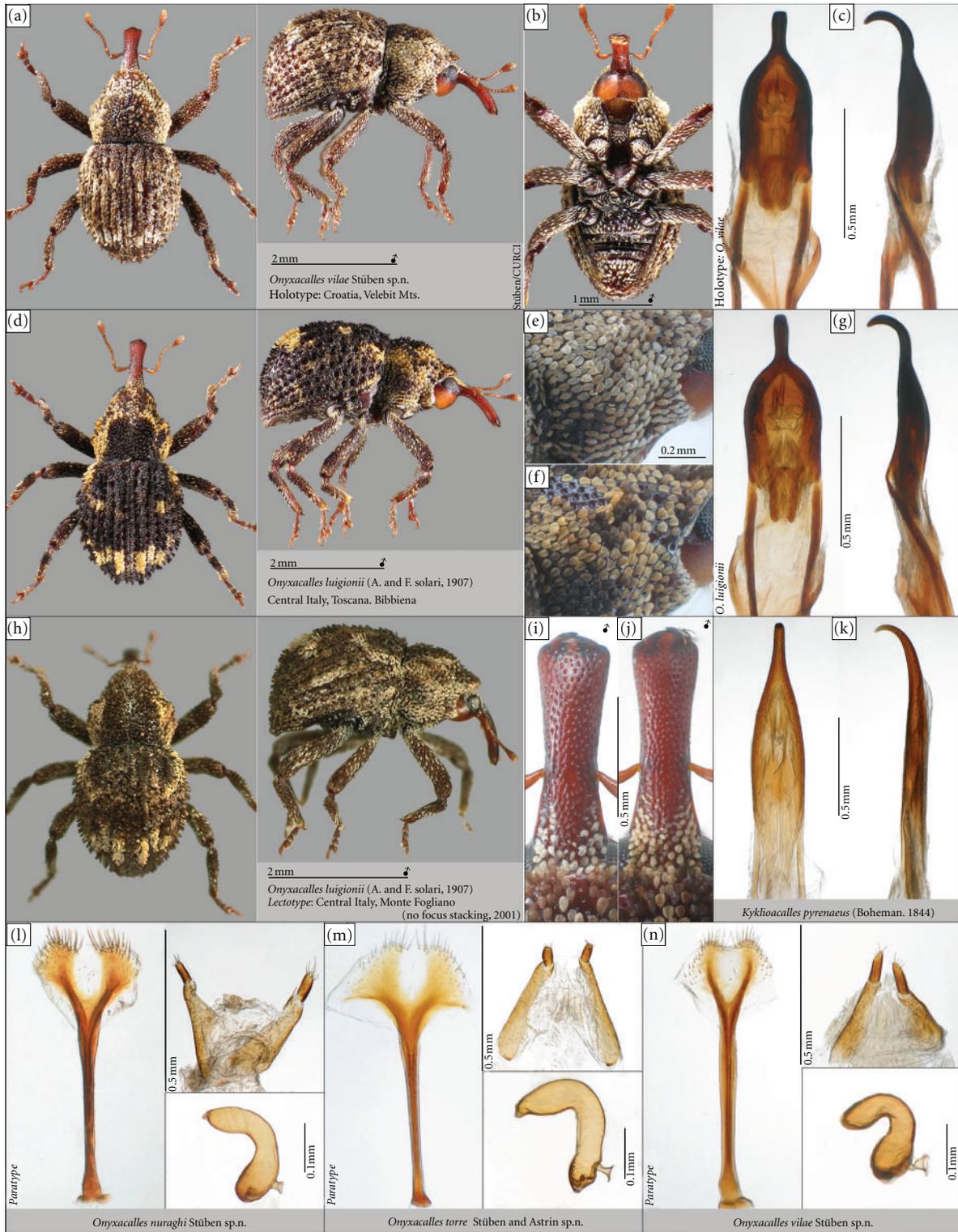


FIGURE 6: (a–c) *O. vilae* sp. n.—habitus (dor./lat./ven.), aedeagus (ven./lat.); (d, g) *O. luigionii*—habitus (dor./lat.), aedeagus (ven./lat.); (h) *O. luigionii* (lectotype)—habitus (dor./lat.); (k) *Kyklioacalles pyrenaicus*—aedeagus (ven./lat.); (l–n) female genital (spiculum ventrale, ovipositor, spermatheca) of *O. nuraghi* sp.n. (l), *O. torre* (m) and *O. vilae* (n). By comparison, bristle of pronotum (lat.)—*O. vilae* (e) versus *O. luigionii* (f); rostrum—*O. vilae* (j) versus *O. luigionii* (i).

at most 2x longer than wide, forming flattened tufts, which have big gaps between them (their distances range from three times the length of bristle); bristles sparse on the second and fourth intervals; striae on the disc and at the sides of elytra clearly narrower than intervals, punctures oblong.

Legs. Long; the marginal front femora reach the base of the rostrum; the hind femora reach the end of the elytral apex. They are covered with predominantly dark brown scales; tibia with long, white, and laterally protruding bristles.

Venter. The 2nd strip-type sternite only a little bit longer than the 3rd, but not longer than sternites 3 and 4 together. 1st sternite of male with a broad depression (Figure 5(b)).

Female Genital. See Figure 6(l).

Aedeagus. Apex (“hook”) of the aedeagus (in ventral view) small, see Figure 5(c).

Etymology. The species name refers to the Nuragic civilization of Sardinia, lasting from the Bronze Age (18th century BC) to the 2nd century AD.

Ecology. *Onyxacalles nuraghi* was discovered by the first author on Sardinia near Lei (Macomer) in the mountains of Marghine in 2010. The seven specimens were shifted under *Quercus* and *Acer* between 500 and 1000 m above sea level.

Distribution. This species is so far only known from the Chain of Marghine, Figure 2.

5.1.2. *Onyxacalles torre* Stüben and Astrin sp. n.

(Figures 5(d)–5(f), 5(m), and 6(m)).

Type Material

Holotype (1♂). France, Corsica (Haute-Corse): Col de Vizavona, 22 km S Corte, 1100 m, 8.10.2001, 42°06′45″N 09°06′49″E, *Fagus* (sift), leg. Stüben-4-, coll. CURCULIO-Institut, D-Mönchengladbach.

Paratypes (8♂, 9♀). Data as for holotype, coll. Stüben, CURCULIO-Institut, D-Mönchengladbach (1♀), Zoologisches Forschungsmuseum Alexander Koenig, D-Bonn (1♂, 1♀).

DNATYPE (1♀). Data as for holotype, coll. ZFMK: ZFMK-DNA-JJ0882, ZFMK-TIS-cF479; GenBank Acc. no 16S: GU988592.

Further Material (1♂). France, Corsica (Haute-Corse): Caporalino 10 km N Corte, 350 m, 7.10.2001, 42°23′08″N 09°11′37″E, *Alnus*, *Fraxinus*, *Quercus* (sift), leg. Stüben-2-, coll. Stüben; 2♂: France, Corsica (Haute-Corse): Tattone,

18 km S Corte, 750 m, 8.10.2001, 42°09′21″N 09°09′43″E, *Castanea* (sift), leg. Stüben-3-, coll. Stüben; 1♂: France, Corsica (Corse-du-Sud): Radicale, 20 km E Ajaccio, 400 m, 9.10.2001, 41°55′31″N 08°58′10″E, 9.X.2001, *Quercus ilex* (sift), leg. Stüben-9-, coll. Stüben; 2♂: France, Corsica (Corse-du-Sud): Cozzano 2 km NE Zicavo, 750 m, 10.10.2001, 41°55′31″N 09°08′31″E, *Castanea* (sift), leg. Stüben-12-, coll. Stüben; 4♂, 4♀: France, Corsica (Corse-du-Sud): Coll de La Vaccia N, 9,5 km S Zicavo, 1150 m, 10.10.2001, 41°49′19″N 09°05′04″E, *Fagus* (sift), leg. Stüben-14-, coll. Stüben.

Differential Diagnosis. The new species from Corsica (France) belongs—morphologically and molecularly—to the *Onyxacalles henoni* group and is distinguished from *Onyxacalles henoni* (Bedel, 1888) [38] from Algeria (Mt. Edough, *loc. typ.*) by the following characteristics.

Onyxacalles torre

- (1) Rostrum finely punctuated towards apex (Figure 5(m)).
- (2) Scales of the elytra predominantly dark brown or black (Figure 5(d)).
- (3) Apex (“hook”) of the aedeagus broader in ventral view and strongly curved (nearly rectangular) in lateral view (Figure 5(f)).

Onyxacalles henoni

- (1*) Rostrum coarsely and densely punctuated towards apex (Figure 5(l)).
- (2*) Scales of the elytra predominantly bright: white, beige, or brown (Figure 5(k)).
- (3*) Apex (“hook”) of the aedeagus smaller in ventral view and not so strongly curved in lateral view (Figure 5(n)).

The new species from Corsica can be distinguished from *Onyxacalles nuraghi* from Sardinia (see above) by (1) contour line of elytra behind the base flatter (in lateral view, Figure 5(d) versus 5(a)), (2) elytra more egg-shaped towards the apex (Figure 5(d) versus 5(a)), and (3) apex (“hook”) of the aedeagus (in ventral view) shorter and wider (Figure 5(f) versus 5(c)). For a comparison with all other species, see the “Key to the species of *Onyxacalles* Stüben, 1999” below.

Description

Length. 3.00–4.00 mm (without rostrum).

Head and Rostrum. Eyes large; rounded towards front and acuminate towards underside of rostrum; frons between eyes as wide as the base of rostrum; rostrum reddish brown, closely covered with white scales at the base; rostrum of male reaching 2/3 length of pronotum and finely punctuated towards apex (Figure 5(m)); rostrum of females reaching 3/4

length of pronotum, slender, shiny, and even more finely punctuated. The last three funicles of the antennae short ovals rounded, the fourth 1.5x, the third 2x, the second 4.5x, and the first conical funicle 2x longer than wide; the elongated club clearly separated from funicles.

Pronotum. Widest at the end of the first third of the pronotum (holotype: 1.17x as wide as long); strongly rounded laterally towards the fore-margin and the base; with a depression at the sides directly behind the fore-margin; disk of pronotum arched, in the middle sometimes with a slight channel-like depression in front of the base. The integument is rich in contrast consisting of round black and dark-brown scales on the disk and in front of the fore-margin, and more or less oval, white scales on the flanks of the pronotum. In the middle of the disk on both sides of the flat depression with elongated, studded, and black bristles in an upright position; with similar placed, but shorter and white bristles on each side of the pronotum; the punctures always covered with scales.

Elytra. Oblong (holotype: 1.31x as long as wide); widest in front of the middle, here with parallel sides or slightly egg-shaped towards the apex; strongly curved in front of the base. Contour line of elytra flatter behind the base in lateral view, the contour line of the elytral slope forming an arc towards the apex. The shiny and predominantly dark brown or black integument with a beige/white crescent-shaped fascia in front of the base and on the elytral slope; sometimes the whole apex can be light brown. Bristles on first and third interval (excluding the suture stripe) 1.5x longer than wide, flattened, and shaping tufts; their distances range from the 2x length of bristles. Bristles sparse on the second and fourth intervals; striae on the disc and at the sides of elytra are small strips, clearly narrower than the intervals, punctures on the disc oblong, round at the sides.

Legs. Long; the marginal front femora reach the base of the rostrum, and the hind femora reach the end of the elytral apex. They are covered with predominantly dark brown and elongated scales; tibia with white/brown and laterally protruding bristles forming fasciae.

Venter. The 2nd strip-type sternite only a little bit longer than the 3rd, but not longer than sternites 3 and 4 together. 1st sternite of male with a broad depression (Figure 5(e)).

Female Genital. See Figure 6(m).

Aedeagus. Apex (hook) of the aedeagus broad in ventral view and strongly curved (nearly rectangular) in lateral view; see Figure 5(f).

Etymology. The species name refers to the Torrean civilization in Corsica during the second millennium BC. The characteristic building of this culture is the “Torre” (tower), the Corsican counterpart of the Sardinian “Nuraghe.”

Ecology. *Onyxacalles torre* was sifted by the first author in the mountains of Corsica and is a nocturnal inhabitant of the dark and shady forests like all other *Onyxacalles*.

Distribution. This species is so far only known from Corsica (France); Figure 2.

5.2. New Species of the *Onyxacalles luigionii* Group

5.2.1. *Onyxacalles vilae* Stüben sp. n.

(Figures 6(a)–6(c), 6(e), 6(i), and 6(n)).

Type Material

Holotype (1♂). Croatia: 20 km S Krasno Polje, Northern Velebit Mts., N44°38'14" E15°05'13", 1185 m, limestone: *Fagus*, 26.7.2004, leg. Stüben-10-, coll. CURCULIO-Institut, D-Mönchengladbach.

Paratypes (1♂, 2♀). Data as for holotype, coll. Stüben, CURCULIO-Institut, D-Mönchengladbach (1♀), Zoologisches Forschungsmuseum Alexander Koenig, D-Bonn (1♀); 1♀: Croatia: Krasno Polje, Northern Velebit Mts., N44°49'40" E15°01'49", 838 m, limestone: *Fagus*, *Quercus*, 25.7.2004 leg. Stüben-7-, coll. Stüben; 1♂: Croatia: 5 km W Krasno Polje, Northern Nord-Velebit Mts., N44°48'49" E14°58'36", 1534 m, limestone: *Fagus*, 26.7.2004, leg. Stüben-8-, coll. Stüben; 1♀: Croatia: 6 km W Krasno Polje, Northern Velebit Mts., N44°48'56" E14°58'08", 1494 m, limestone: *Fagus*, 26.7.2004, leg. Stüben-9-, coll. Stüben; 1♂: Croatia: 12 km S Krasno Polje; Northern Velebit Mts., N44°43'00" E14°59'42", 1414 m, limestone: *Fagus*, 27.7.2004, leg. Stüben-14-, coll. Stüben.

DNA type (1♂). Croatia: 8 km E Karlobag, Velebit Mts., Stupacinovo, N44°32'41" E15°09'58", 1049 m, limestone: *Fagus*, 14.07.2007, leg. Stüben-27-, coll. ZFMK: ZFMK-DNA-JJ0195, ZFMK-TIS-cHR339; GenBank Acc. no COI: EU286512, 16S: EU286348.

Further Material (9♂, 7♀). France, Isère, 2 km SE Lans en Vercors, Montagne de Lans, 45°06'40"N 05°36'25"E, 1391 m, 23.7.2011, Kalk: *Fagus* (beaten), leg. Stüben-2-, coll. Stüben; 3♂, 3♀: France, Isère, NW Lans en Vercors: near Autrars, Parc Regional du Vercors, 45°14'12"N 05°34'58"E, 1370 m, 23.7.2011, Kalk: *Fagus* (beaten), leg. Stüben-5-, coll. Stüben.

Differential Diagnosis. The new species from Croatia (Velebit Mts., *loc. typ.*) belongs—morphologically and molecularly—to the *Onyxacalles luigionii* group and is distinguished from *Onyxacalles luigionii* (A. & F. Solari, 1907) [32] from Central Italy (Monte Fogliano, *loc. typ.*) by the following characteristics.

Onyxacalles vilae

- (1) Rostrum of the male broader, 2.8x as long as wide (as measured by apex); punctures not so densely packed

in front of the apex (separated by flat intervals) Figure 6(i).

- (2) Bristles of the low-contrast elytra on first and third intervals (excluding the sutural stripe) longer and more slender; their distance is larger (Figure 6(a)).
- (3) Scales of the white fascia at the sides of the pronotum (behind the base) predominantly oblong (Figure 6(e)).
- (4) Median lobe of aedeagus smaller, 1.64x as long as wide; apex (“hook”) a little bit shorter (in ventral view), flatter, and not so strongly curved in lateral view (Figure 6(c)).

Onyxacalles luigionii

- (1*) Rostrum of the male more slender, 3.1x as long as wide; punctures mainly dense towards the apex (only separated by small ridges) Figure 6(j).
- (2*) Bristles of high-contrast elytra on the on first and third intervals shorter, broader (towards the apex of bristle), and more dense, clearly visible on the white fascia of the elytral slope (Figures 6(d) and 6(h)).
- (3*) Scales of the white fascia at the sides of the pronotum (behind the base) predominantly round (Figure 6(f)).
- (4*) Median lobe of aedeagus broader, 1.93x as long as wide; apex (“hook”) of the aedeagus longer (in ventral view), strongly (nearly rectangular) curved in lateral view. Internal structure (endophallus) of the sac different (Figure 6(g)).

For a comparison with all other species see below the “Key to the species of *Onyxacalles* Stüben, 1999.”

Description

Length. 2.40–3.20 mm (without rostrum).

Head and Rostrum. Eyes large; rounded ovally towards front and acuminate towards underside of rostrum; frons between eyes as wide as the base of rostrum; rostrum reddish brown, closely covered with white and oval scales at the base; rostrum of male 2.8x as long as wide (as measured by apex) and finely punctuated towards apex, here separated by flat intervals (Figure 6(i)); rostrum of female clearly longer, slender, shiny, and even more finely punctuated (without punctures in front of the apex). The last funicles of antennae nearly trapezoidal, the funicles 4–6 short oval, the third funicle 1.3x, the second 3x, and the first conical funicle 1.5x longer than wide; the elongated club not clearly separated from the 7th trapezoid funicle.

Pronotum. Widest at the end of the first third of the pronotum (holotype: 1.12x as wide as long); well rounded laterally towards the fore-margin and the base; with a slight depression at the sides directly behind the fore-margin; disk of pronotum arced, without a channel or a flat depression

in the middle. The integument not so rich in contrast, consisting of round, brown scales on the disk and off-white, predominantly oblong scales at the sides of the pronotum (behind the base, Figure 6(e)). In the middle of the disk with elongated brown bristles in an upright position; with a similar, but white tuft of bristles on each side of the pronotum; the deep and dense punctures covered with scales.

Elytra. Short oval (holotype: 1.19x as long as wide); widest at the end of the first fourth in front of the elytral base; here laterally strongly rounded directly in front of the base; ovally rounded towards the apex. Contour-line of elytra flatter behind the base in lateral view, the contour line of the elytral slope forming a circular arc towards the apex. Bristles of the low-contrast elytra on first and third intervals (excluding the sutural stripe) slender, 2x–3x as long as wide, their distance reaching the double length of bristle, and forming tufts only in front of the base and on the elytral slope; the uprightly protruding bristles on the second and fourth intervals have wider gaps between them (their distances range from three- to fourfold length of bristle); the scales on the intervals do not cover the underground completely; striae on the disc broad, but not broader than the intervals, reaching the width of the intervals at the sides of elytra (but often covered by scales); punctures deep and rounded.

Legs. Long; the marginal front femora reach the base of the rostrum, and the hind femora reach the end of the elytral apex. They are covered with predominantly brown scales; tibia with short, white, and laterally protruding bristles.

Venter. The 2nd strip-type sternite only a little bit longer than the 3rd, but not longer than sternites 3 and 4 together. 1st sternite of male with a broad depression (Figure 6(b)).

Female Genital. See Figure 6(n).

Aedeagus. Median lobe of aedeagus small, 1.64x as long as wide; see Figure 6(c).

Etymology. The species name refers to a “Vila” (*fairy*) in the Velebit Mts. This massif has a similar relevance for Croatians to Olympus for Greeks or the Fujiyama for the Japanese. In Croatia, the mystical Velebit Mts. range is famous for its fairies, the most celebrated called “Vila Velebita” (*The Fairy of Velebit*).

Ecology. *Onyxacalles vilae* was sifted by the first author in the Velebit mountains of Croatia under *Fagus* and *Quercus* between 800 and 1600 m above sea level.

Distribution. A complete distribution map will be given in a separate faunistic study in the future, but this species was also sifted by the author in the Montagne de Lans near Lans en Vercors (France: Isère)—on limestone and under *Fagus*, too (N45°06′45″ E05°36′21″, 1352 m). Working hypothesis: It could be possible that all specimens of the “Alpine Arc”—between Grenoble and the Velebit mountains—belong to this

new species and can be separated from the Central Italian populations of *Onyxacalles luigionii* (cf. Figure 3).

6. Key to the Species of *Onyxacalles* Stüben, 1999

- (1) Smaller species with an ovaly rounded habitus, legs shorter, femora reach the base of the rostrum; rostrum shorter and broader; if tufts of bristles exist on the elytral slope, these are only densely placed (not tapered). Distribution: continent of Western Palaearctic.

Subgenus: *Onyxacalles* s. str. 2

- (1*) Larger species with a more “elliptical” habitus and with long legs, femora reach the insertions of the antennae; rostrum very long and slender; the tapered tufts of bristles on the elytral slope strongly protruding (Figures 8(b)–8(d)). Distribution: Western Canary Islands.

Subgenus: *Araneacalles* Stüben and Astrin, 2010 ... 16

- (2) Apex of the aedeagus regularly rounded in lateral view: Figures 6(c) and 6(g) (both species without distinctive tufts of bristles on the uneven elytral intervals, only with densely placed bristles in one or two rows).

Luigionii group 2

- (2*) Apex of the aedeagus with a second, separated peak in lateral view (cf. Figures 9(a)–9(l)) (most species with more or less characteristic tufts of bristles on the elytra).

..... 4
— *Luigionii* group —

- (3) Rostrum of the male more slender, 3.1x as long as wide; punctures mainly dense towards the apex (only separated by small ridges) (Figure 6(j)). Bristles of high-contrast elytra on the 1st and 3rd intervals shorter, broader (towards the apex of bristle), and more dense (Figures 6(d) and 6(h)). Median lobus of aedeagus broader, 1.93x as long as wide; apex (“hook”) of the aedeagus longer (in ventral view), strongly (nearly rectangular) curved in lateral view. Internal structure (endophallus) of the sac different (Figure 6(g)). Distribution: Central and Southern Italy (Figure 3).

Onyxacalles luigionii (A. & F. Solari, 1907) [32]
= ? *Onyxacalles porcheti* [39] (Figure 8(e), Pyrenees)

- (3*) Rostrum of the male broader, 2.8x as long as wide (as measured by apex); punctures not so densely packed in front of the apex (separated by flat intervals) (Figure 6(i)). Bristles of the low-contrast elytra on the 1st and 3rd intervals (excluding the sutural stripe) longer and more slender; their distance larger

(Figure 6(a)). Median lobus of aedeagus smaller, 1.64x as long as wide; apex (“hook”) a little bit shorter (in ventral view), flatter, not so strongly curved in lateral view (Figure 6(c)). Distribution: Croatia (l.t.), France: Isère (Figure 3).

Onyxacalles vilae Stüben sp. n.

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- (4) Pronotum levelled, “triangular” and stubby, strongly broadened just behind the base; the base 2x longer than the fore-margin (this characteristic is not so pronounced in *O. gibraltarensis*; however, this species can be clearly separated from all other *Onyxacalles* s. str. by the completely rounded sides of the aedeagus (Figure 9(a)), see digit 5). Distribution: Southern France, Iberian Peninsula, Morocco.

Portusveneris group 5

- (4*) Pronotum more arched and marginally broader than long, widest at the end of the first third; the base at most 1.5x longer than the fore-margin. Distribution: Algeria, Tunisia, Western Spain, West Mediterranean Islands, Southeastern Europe, Turkey.

..... 9
— *Portusveneris* group —

- (5) Pronotum more slender, clearly separated from elytra; body outline broadly similar to the species of the *henoni* group (see digit 4*), but easy to distinguish from these species by the completely rounded sides of the aedeagus. Habitus (Figure 7(a)). Aedeagus (Figure 9(a)). Distribution: Southern Spain, Northern Morocco (Figure 4).

Onyxacalles gibraltarensis Stüben, 2002

- (5*) Pronotum widest directly behind the base and elytra widest directly in front of the base; therefore, pronotum and elytra do not seem separated (Figures 7(b)–7(e)).

..... 6

- (6) Elytra egg-shaped towards the apex (Figure 7(b)); Aedeagus (Figure 9(b)). Distribution: Southern France, Iberian Peninsula, Morocco (Figure 4).

Onyxacalles portusveneris (Mayet, 1903)

[27]

- (6*) Elytra oval or with more or less parallel sides (Figures 7(c)–7(e)).

..... 7

- (7) Male with a split midtibia spine at the apex; uneven elytral intervals without tufts of bristles. Habitus (Figure 7(c)). Aedeagus (Figure 9(c)). Distribution: Southern Spain (Figure 4).

Onyxacalles seguraensis Stüben, 2003

- (7*) Male without a split midtibia spine at the apex; uneven elytral intervals with tufts of bristles.

..... 8



FIGURE 7: (a–e): **Portusveneris group**—*O. gibraltarensis* (a), *O. portusveneris* (b), *O. seguraensis* (c), *O. maginaensis* (d), and *O. bermejaensis* (e); (f): **Incertae sedis**—*O. denominandus*; (g–h): **Henoni group** (see also next figures)—*O. croaticus* (g) and *O. valencianus* (h); all habitus (dor./lat.).

- (8) Punctures at the sides of elytra fine and slender; bristles on the first four intervals of the elytral slope in single row. Habitus (Figure 7(d)). Aedeagus (Figure 6(d)). Distribution: Southern Spain (Figure 4).

***Onyxacalles maginaensis* Stüben, 2004**

- (8*) Punctures at the sides of elytra broader and deeper; bristles on the third interval of the elytral slope

densely placed, forming a pronounced tuft at the level of the white fascia. Habitus (Figure 7(e)). Aedeagus (Figure 9(e)). Distribution: Southern Spain (Figure 4).

***Onyxacalles bermejaensis* Stüben, 2001**

- (9) Pronotum with a deep midgroove and with strong concavities on each side; a species from Turkey.



FIGURE 8: (a): **Henoni group**—*O. hannibali* (see also the other species of this group: Figures 5(a), 5(d), 5(g), 5(k)); (b–d): subgenus: **Araneacalles**—*O. neglectus* (b), *O. verrucosus* (c), and *O. ringeli* (d); (e): *O. porcheti* (perhaps *O. luigionii*); (f): *Kyklioacalles pyrenaicus*; (g) *K. fausti*; (h) *K. saccoi*; all habitus (dor./lat.).

Habitus (Figure 7(f)). Aedeagus (Figure 9(f)). Distribution: Turkey.

Onyxacalles denominandus (A. & F. Solari, 1907) [32]
= ? *Onyxacalles amasyaensis* Wolf, 2001

(9) Pronotum behind the base at most with a flat depression or a hinted channel; mainly West Mediterranean species, only one species from southeastern Europe.

Henoni group 10

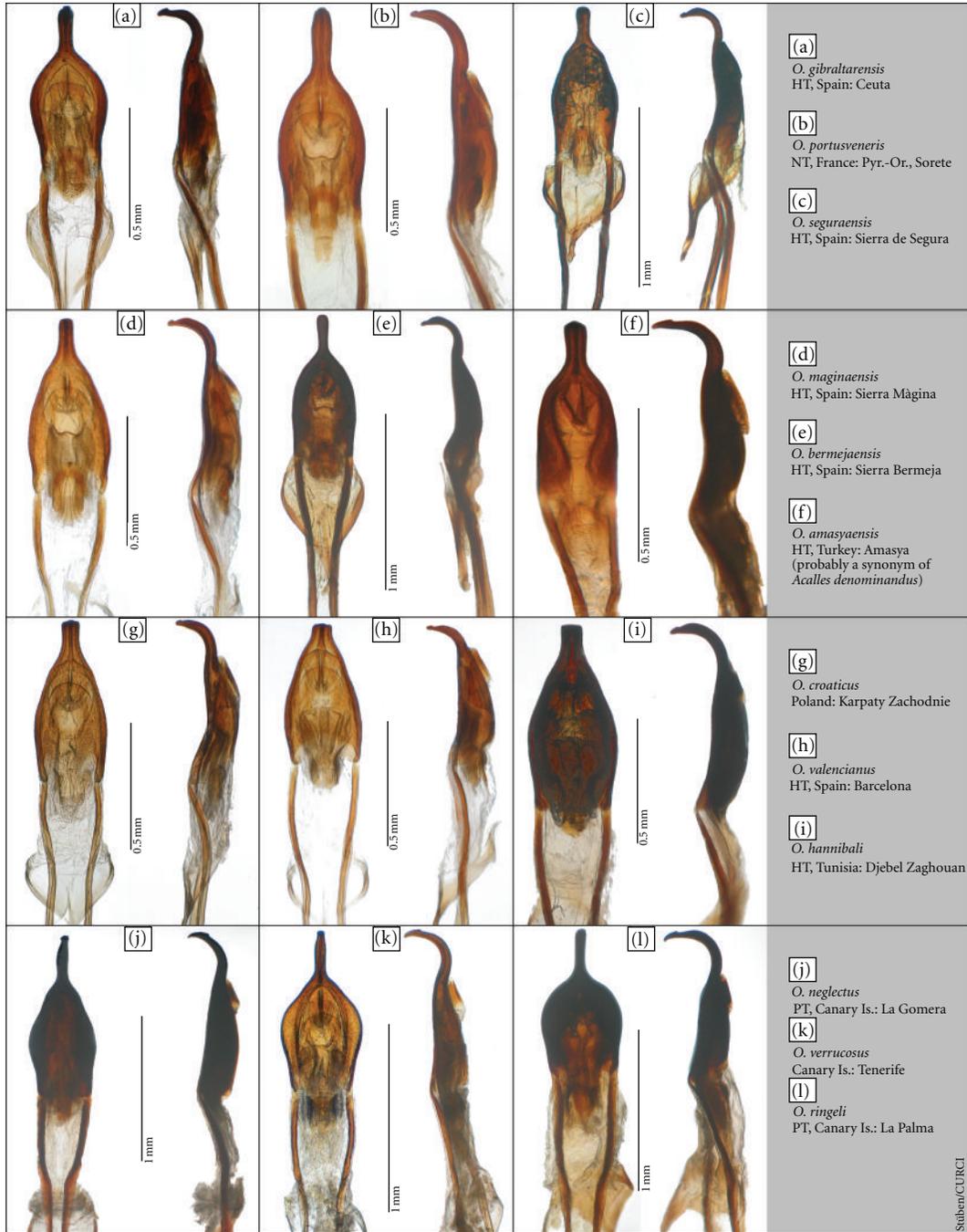


FIGURE 9: (a–d): **Portusveneris group**—*O. gibraltarensis* (a), *O. portusveneris* (b), *O. seguraensis* (c), *O. maginaensis* (d), and *O. bermejaensis* (e); (f): **Incertae sedis**—*O. amasyaensis*; (g–i): **Henoni group**—*O. croaticus* (g), *O. valencianus* (h), *O. hannibali* (i) (see also the other species of this group: Figures 5(c), 5(f), 5(j), 5(n)); (j–l): subgenus: **Araneacalles**—*O. neglectus* (j), *O. verrucosus* (k), and *O. ringeli* (l).

— **Henoni group** —

(10) Elytra with superelevated and in tubercles dissected intervals; a species from southeastern Europe, which is added to the *henoni* group preliminary on the basis of a similar form of the aedeagus. Habitus (Figure 7(g)). Aedeagus (Figure 9(g)). Distribution: East and Southeast Europe [31].

Onychacalles croaticus (H. Brisout de Barneville, 1867) [10]

(10) Elytra flat, without tubercles.

..... 11

(11) Elytra and pronotum (almost) without tufts of bristles; these single, beaded bristles placed in a row.

..... 12

- (11*) Elytra on the intervals 1 and 3 and pronotum at the sides with tufts of bristles; these bristles densely placed in 2-3 rows, forming tufts at regular intervals.

..... 13

- (12) Elytral bristles short, shovel-shaped and densely placed (at most 1.3x as long as wide); elytra rich in contrast (colored); apex of aedeagus strongly curved in lateral view. Habitus (Figure 5(g)). Aedeagus (Figure 5(j)). Distribution: Spain, Majorca (Figure 2).

***Onyxacalles balearicus* Stüben, 2005**

- (12*) Elytral bristles more slender, at least 2x as long as wide and their distance large; elytra poor in contrast; apex of aedeagus flatter curved in lateral view. Habitus (Figure 6(n)). Aedeagus (Figure 9(h)). Distribution: Eastern Spain (Figure 2).

***Onyxacalles valencianus* Germann, 2005**

- (13) Disc of pronotum with a channel from the base towards the flat sector in front of the fore-margin; elytra of male with parallel sides in the middle sector (dorsal view). Habitus (Figure 5(a)). Aedeagus (Figure 5(c)). Distribution: Italy, Sardinia (Figure 2).

***Onyxacalles nuraghi* Stüben sp. n.**

- (13) Disc of pronotum at most with a flat hollow behind the base; elytra of male broader and stronger (short ovaly) rounded (slightly “egg-shaped”).

..... 14

- (14) Elytral intervals only with a few bristles and small tufts; elytra poor in contrast. Habitus (Figure 8(a)). Aedeagus (Figure 9(i)). Distribution: Tunisia (Figure 2).

***Onyxacalles hannibali* Germann, 2004**

- (14*) Elytral intervals studded with bristles and with numerous distinctive tufts; elytra rich in contrast.

..... 15

- (15) Rostrum coarsely and densely punctuated towards apex (Figure 5(l)); scales of the elytra predominantly bright: white, beige, or brown (Figure 5(k)); Apex (“hook”) of the aedeagus smaller in ventral view and not so strongly curved in lateral view (Figure 5(n)). Distribution: Algeria, Mt. Edough (Figure 2).

***Onyxacalles henoni* [38]**

- (15*) Rostrum finely punctuated towards apex (Figure 5(m)); scales of the elytra predominantly dark brown or black (Figure 5(d)); apex (“hook”) of the aedeagus broader in ventral view and strongly curved (nearly rectangular) in lateral view (Figure 5(f)). Distribution: France, Corsica (Figure 2).

***Onyxacalles torre* Stüben and Astrin sp. n.**

— Subgenus: *Araneacalles* —

- (16) Punctures of the 1st and 2nd elytral striae rounded, pothole-like, and as wide as the intervals; the underground of elytra in front of the middle on the 8th and 9th intervals with scales, not shiny; fore-margin of pronotum with a curved up collar. Habitus (Figure 8(b)). Aedeagus (Figure 9(j)). Distribution: Canary Is., La Gomera (l.t.), El Hierro (Figure 4).

***Onyxacalles neglectus* Kulbe, 1999**

- (16*) Punctures of the 1st and 2nd elytral striae elongated, clearly smaller than intervals; the underground of elytra in front of the middle on the 8th and 9th intervals without scales, shiny; fore-margin of pronotum without a curved up collar.

..... 17

- (17) Punctures at the extreme striae slender, the intervals broader; elytra widest in front of the middle, egg-shaped. Habitus (Figure 8(c)). Aedeagus (Figure 9(k)). Distribution: Canary Is., Tenerife (l.t.), El Hierro (Figure 4).

***Onyxacalles verrucosus* (Wollaston, 1863) [40]**

- (17*) Punctures at the extreme striae larger and rounded, not broader than intervals; elytra oval, widest in the middle. Habitus (Figure 8(d)). Aedeagus (60). Distribution: Canary Is., La Palma (Figure 4).

***Onyxacalles ringeli* Kulbe, 1999**

Acknowledgments

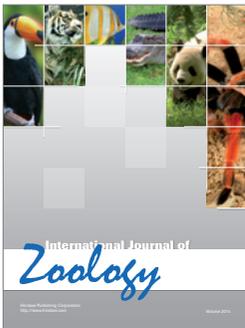
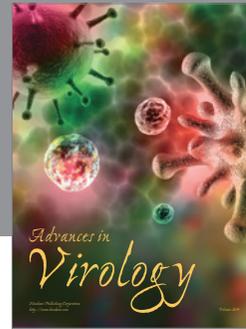
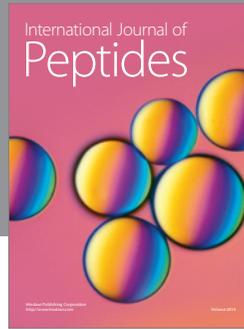
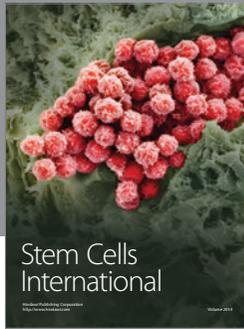
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