A revision of *Othius* STEPHENS of the Atlantic Islands.
III: Further records, new species, phylogenetics, and colonization
(Insecta: Coleoptera: Staphylinidae: Xantholininae)

With 4 Figures and 1 Table

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Abstract. Further records of *Othius* from Madeira and the Canary Islands are presented. *Othius coif-faiti* LOHSE and its synonym *O. pseudolapidicola* COIFFAIT are synonymized with *O. philonthoides* WOLLASTON. *O. microphallus* spec. nov. is described from Tenerife and compared with its closest relative, *O. intermedius* KORGE; primary and secondary sexual characters are figured. A phylogenetic analysis of Atlantic *Othius* shows that, not considering the recent introduction of *O. punctulatus* (GOEZE) to the Canary Islands, both Madeira and the Canarian archipelago are inhabited by two monophyletic groups and were colonized twice by species of *Othius*. The phylogeny of Atlantic *Othius* and the colonization of the islands are discussed.

Introduction

Since the recent revisions of the species of *Othius* STEPHENS of Madeira and the Canary Islands (ASSING & WUNDERLE 1995; ASSING 1997a), *O. punctulatus* (GOEZE), a species widely distributed in the Western Palaearctic region and apparently a recent introduction, has for the first time been recorded from the Canary Islands (ASSING 1997b). In addition, further material of the endemic species has become available for examination. As faunistic data are still rather scarce for most Atlantic *Othius*, these records are here presented. Moreover, a larger number of recently collected specimens of *O. philonthoides* WOLLASTON and *O. coiffaiti* LOHSE, respectively, allowed the question to be reconsidered, whether or not these taxa represent distinct species.
The material listed for *O. intermedius* KORGE in ASSING (1997a) included 3 specimens from the Pico del Ingles (Anaga mountain range, Tenerife) which were clearly smaller than average *O. intermedius* and also had a smaller aedeagus. However, since only two ♂♂ and one ♀ were available, the possibility that these specimens represented extreme or aberrant forms could not be ruled out and they were tentatively treated as *O. intermedius*. In the course of a revision of Western Palaearctic *Othius*, six further specimens collected at the same locality were recently discovered in the collections of the Staatliches Museum für Naturkunde in Stuttgart, all of them externally exactly like the specimens studied before and the three males with a clearly smaller aedeagus than in *O. intermedius*. They are here hypothesized to represent a distinct species, also because with more material available, further distinguishing characters were observed.
Based on ingroup comparison it was previously assumed that the Canarian *Othius* species form two monophyletic groups, suggesting that the Canary Islands were colonized twice (ASSING 1997a). (The recent introduction of *O. punctulatus* is here neglected.) Yet, these conclusions could only be regarded

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as tentative in the absence of a revision of continental species of the Western Palaearctic region. For the same reason, even less was known about the colonization of the Madeiran archipelago. With a recent revision of the continental species now available, the phylogenetics of Atlantic *Othius* and the colonization of the archipelagos are here reexamined.

Material

Material from the following institutions and private collections was examined:

DEI   Deutsches Entomologisches Institut, Eberswalde (L. Zerche)
IRSNB   Institut Royal des Sciences Naturelles de Belgique, Bruxelles (D. Drugmand)
NHMW   Naturhistorisches Museum Wien (H. Schillhammer)
SMNS   Staatliches Museum für Naturkunde in Stuttgart (W. Schawaller)
cAss   author's private collection
cGil   Private collection G. Gillerfors, Varberg
cOro   Private collection P. Oromi, La Laguna
cSch   Private collection M. Schülke, Berlin
cWun   Private collection P. Wunderle, Mönchengladbach

Measurements

The measurements are indicated in mm and abbreviated as follows:
HW: maximal head width; HL: head length from front margin of clypeus to neck; PW: maximal width of pronotum; PL: length of pronotum along median line; EL: length of elytra from apex of scutellum to elytral hind margin; TiL: length of metatibiae (external aspect from knee to insertion of first metatarsomere); TaL: length of metatarsi (claws not included); TL: total length from apex of mandibles to hind margin of tergum VIII.

Additional records of *Othius* from Madeira

Othius strigulosus WOLLASTON

2 ♂♂, 3 larvae (second instar), Rabacal, 1 000 m, mixed stand of *Laurus* and *Erica* in northern expo- sition, 23. III. 1996, leg. Assing (cAss); 1 ♂, same data, leg. Zerche (DEI); 2 ♂♂, 1 larva, (second instar), above Rabacal, 1 300 m, mixed stand of *Erica* and *Vaccinium* in northern exposition, 27. III. 1996, leg. Assing (cAss); 2 ♂♂, Rabacal, 950 m, *Laurus* wood, 2. IV 1996, leg. Lompe (cAss); 1 ♀, Rabacal, 1 000 m, 27. X. 1997, leg. Lompe (cAss); 1 larva (third instar), Rabacal, 950 m, mixed stand of *Laurus, Vaccinium* and *Erica*, 3. IV 1996, leg. Assing (cAss); 1 ♀, Ribeira da Janela, N Fanal, 900 m, *Laurus* wood, 25. III. 1996, leg. Zerche (DEI); 5 ♂♂, 1 ♀, Ribeira da Janela, above Fanal, 1 300 m, mixed stand of *Laurus, Vaccinium, Erica,* 25. III. 1996, leg. Assing (cAss); 1 ♂, same data, leg. Zerche (DEI); 3 ♂♂, E Encumeada, path to Pico Ruivo, 1 500 m, stand of *Erica* with scattered *Laurus,* 26. III. 1996, leg. Assing (cAss); 1 ♀, same data, leg. Zerche (DEI); 1 ♂, E Encumeada, below Pico do Jorge, 1 300 m, below *Laurus,* 30. III. 1996, leg. Assing (cAss); 2 ♀♀, same data, but mixed stand of *Erica, Vaccinium, Laurus* (cAss); 1 ♂, 2 larvae (third instar), 1 larva (second instar), S San- tana, Achada do Teixeira, 1 350 m, stand of old *Erica,* 29. III. 1996, leg. Assing (cAss); 1 ♂, 2 ♀♀, Achada do Teixeira, 1 350 m, 19. X. 1997, leg. Lompe (cAss); 2 ♂♂, Pico Arieiro, coll. Kraatz (DEI); 1 ♂, Madeira, coll. Kraatz (DEI); 1 ♀, Schmitz [?], coll. Fauvel (IRSNB); 1♀, Rabacal, coll. Fauvel (IRSNB); 2 ♂♂, Moniz, coll. Fauvel (IRSNB, cAss); 1 ♂, 1 ♀, Le Mout., coll. Fauvel (IRSNB); 1♂, 1♀, S. Anna, coll. Fauvel (IRSNB); 2 ♂♂, 2 ♀♀, Pico Arieiro, coll. Fauvel (IRSNB); 1♀, Caramujo,

IV 1952, leg. Pecoud, coll. Fagel (IRSNB); 1 ♀, Funchal, leg. Pasquale (NHMW); 1 ♀, Pico do Jorge, 1200–1600 m, 11.IV 1994, leg. Donabauer (cAss); 1 ♂, 'Madera' (NHMW); 1 ♂, 2 ♀♀, 'Madère', coll. Fagel (IRSNB).

O. strigulosus is apparently the most widely distributed species of Madeiran *Othius*. It has been recorded from numerous localities (1000–1500 m) from the Ribeira da Janela in the northwest to the surroundings of Funchal in the southeast (ASSING & WUNDERLE 1995; new records).

Othius jansoni WOLLASTON

1 ♂, Rabacal, 1000 m, 17.X.1997, leg. Lompe (cAss); 1 ♂, 4 larvae (third instar), summit of Pico Ruivo, 1850 m, northern slope, *Erica* litter, 29.III.1996, leg. Assing (cAss); 1 ♂, same locality and date, western slope, leg. Zerche (DEI); 1 ♂, 2 ♀♀, 3 larvae (third instar), path from Achada do Teixeira to Pico Ruivo, 1700 m, grass and fern litter in the shadow of big rocks, 29.III.1996, leg. Assing (cAss); 1 ♂, Schmitz [?], coll. Fauvel (IRSNB); 1 ♂, 1 ♀, Queimadas, 900 m, 25.X.1997, leg. Lompe (cAss); 1 ♀, Ribeiro Frio, coll. Fauvel (IRSNB); 2 ♂♂, Pico Arieiro, coll. Fauvel (IRSNB); 1 ♀, 'Poyzo', coll. Fauvel (IRSNB); 1 ♀, 'Moniz', coll. Fauvel (IRSNB); 1 ♂, 1 ♀, [locality not specified] coll. Fauvel (IRSNB); 1 ♂, 'Madère', coll. Fagel (IRSNB).

O. jansoni has been found in several localities from Rabacal in the west to the Pico Arieiro and is now also known from the Pico Ruivo (ASSING & WUNDERLE 1995; new records). The two records indicated in ERBER & HINTERSEHER (1988) from Paul da Serra (Rib. d. Delgado) and Bica da Cana are here confirmed (specimens from coll. Erber examined).

Othius arieiroensis PALM

3 ♂♂, 7 ♀♀, Pico Arieiro, 1600 m, mixed stand of *Erica* and *Vaccinium* in southern exposition, 21.III.1996, leg. Assing (cAss); 3 ♀♀, same data, leg. Zerche (DEI).

Aside from a single record from the surroundings of Funchal, this species has become known only from the type locality.

Othius baculifer ASSING & WUNDERLE

10 ♂♂, 1 ♀, E Encumeada, path to Pico Ruivo, 1500 m, stand of *Erica* with scattered *Laurus,* 26.III.1996, leg. Assing (cAss); 2 ♂♂, 3 ♀♀, above Rabacal, 1300 m, mixed stand of *Erica* and *Vaccinium* in northern exposition, 27.III.1996, leg. Assing (cAss); 3 ♂♂, 3 ♀♀, same data, leg. Zerche (DEI); 3 ♂♂, 7 ♀♀, summit of Pico Ruivo, 1850 m, northern slope, *Erica* litter, 29.III.1996, leg. Assing (cAss); 2 ♂♂, 1 larva (third instar), path from Achada do Teixeira to Pico Ruivo, 1700 m, grass and fern litter in the shadow of big rocks, 29.III.1996, leg. Assing (cAss).

O. baculifer was previously known only from Bica da Cana, Rabacal and Pico Arieiro (ASSING & WUNDERLE 1995). At least one of the ♀♀ collected on 29.III.1996 had a mature egg in the ovaries.

Additional records of *Othius* from the Canary Islands

Othius brachypterus WOLLASTON

2 ♂♂, [1 teneral], La Gomera, Bosque del Cedro, 1000 m, 1.IV 1969, leg. Decelle (IRSNB); 1 ♂, Gomera, El Jardin, 12.VIII.1977, leg. Oromi (cAss); 1 ♂, 1 ♀, same locality, 10.VIII.1978, leg. Oromi (cOro); 1 ♀, same locality, 28.VIII.1985, leg. Oromi (cOro); 1 ♀, El Cedro, 7.VIII.1978, leg. Oromi (cOro); 2 ♂♂, La Gomera, Laguna Grande, 1250 m, Laurisilva, 2.XII.1996, leg. Schülke (cSch).

Othius microphtalmus COIFFAIT

1 ♂, La Gomera, Barranco del Cedro, Eremita d. N. S. de Lourdes, 940 m, 2. XII. 1996, leg. Schülke (cSch); 1 ♂, 1 ♀, La Gomera, Laguna Grande, 1250 m, Laurisilva, 2. XII. 1996, leg. Schülke (cSch, cAss).

Othius neglectus PALM

1 ♂, 3 ♀♀, Gran Canaria, Bco. de la Virgen, 500 m, 20. XII. 1997, leg. Assing (cAss); 1 ♂, 2 ♀♀, same data, leg. Wunderle (cWun); 1 ♂, Gran Canaria, N Cruz de Tejeda, 1600 m, 26. XII. 1997, leg. Assing (cAss); 26 ♂♂, 27 ♀♀, Gran Canaria, S Las Lagunetas, Bco. de la Mina, 1200 m, 21. XII. 1997, leg. Assing (cAss); 6 ♂♂, 13 ♀♀, same data, leg. Wunderle (cWun).

In *O. neglectus,* remarkable intraspecific variation particularly of size was observed, as is shown in the following measurements (range): HL: 0.68–1.03; HW: 0.59–0.95; PW: 0.66–0.98; PL: 0.88–1.85; EL: 0.43–0.68; TiL: 0.56–0.80; TaL: 0.47–0.63; TL (abdomen fully extended): 5.3–7.7. The extremes deviated from the means by up to 25%!
The species is endemic to Gran Canaria, where it is apparently very local. It is now known from four localities in the northern and central parts of the island (ASSING 1997a; new records). The ovaries of one dissected ♀ collected on 20. XII. contained a mature egg.

Othius philonthoides WOLLASTON

O. coiffaiti LOHSE, 1963, **syn. nov.**
O. pseudolapidicola COIFFAIT, 1964, **syn. nov.**

3 ♂♂, Hierro, El Golfo, 800–1000 m, 8. III. 1983, leg. Besuchet (MHNG); 2 ♂♂, Hierro, El Golfo, 1000 m, 6. III. 1983, leg. Besuchet (MHNG, cAss); 1 ♂, Hierro, El Pinar, 1100 m, 5. III. 1983, leg. Besuchet (MHNG); 1 ♂, Hierro, Mirador Jinama, 1300 m, 8. III. 1983, leg. Besuchet (cAss); 1 ♀, Hierro, Amoco, 900 m, 7. III. 1983, leg. Besuchet (cAss); 1 ♂, Hierro, El Golfo, *Laurus* wood, leg. Franz (NHMW); 1 ♂, La Gomera, Pajarito, 2. I. 1984, leg. Gillerfors (cGil); 1 ♂, La Palma, S La Cumbrecita, 800–1000 m, 10. III. 1990, leg. Schawaller (SMNS); 5 ♂♂, 6 ♀♀, Gran Canaria, Bco. de la Virgen, 500 m, 20. XII. 1997, leg. Assing (cAss); 3 ♂♂, same data, leg. Wunderle (cWun); 4 ♂♂, 7 ♀♀, Gran Canaria, N Cruz de Tejeda, 1600 m, *Pinus canariensis* wood, 25. XII. 1997, leg. Assing (cAss); 3 ♂♂, same data, leg. Wunderle (cWun).

There had been doubts that *O. coiffaiti* LOHSE should represent a species distinct from *O. philonthoides* WOLLASTON (ASSING 1997a). However, with only one ♂ from Gran Canaria – the type locality of the latter – available for study, they had tentatively been treated as distinct species. Based on a greater number of recently collected specimens from Gran Canaria and on further material from Hierro, both taxa were reexamined. As constant differences were observed neither in external morphology nor in the genitalia, *O. coiffaiti* LOHSE and consequently also its synonym *O. pseudolapidicola* COIFFAIT are here synonymized with *O. philonthoides* WOLLASTON.
O. philonthoides is now known from Gran Canaria, Hierro, Gomera and La Palma (first record). In two Gran Canarian localites (Bco. de la Virgen; Cruz de Tejeda) it was collected together with second and third instar *Othius* larvae in December. These larvae, however, could also refer to *O. neglectus* PALM, which, too, was present in these localities, though only one adult specimen of that species was found at Cruz de Tejeda.

Othius intermedius KORGE

2 ♀♀, Tenerife, Aguamansa, 1100 m, 16. III. 1969, leg. Decelle (IRSNB); 1 ♂, Tenerife, Orotava valley, Aguamansa, 1080 m, 25. XII. 1997, leg. Stüben & Bahr (cAss); 2 ♂♂, Tenerife, Montana Cabeza de Toro, 1300 m, 26. XI. 1996, leg. Schülke & Grünberg (cSch); 2 ♀♀, Tenerife, Esperanza, Las Rosas, 1000 m, 26. XI. 1996, leg. Schülke & Grünberg (cSch); 2 ♂♂, Esperanza, 1500 m, 13. III. 1983, leg. Besuchet (MHNG).

Othius zerchei ASSING

1 ♂, 1 ♀, Tenerife, Ruigomez, 900 m, 12. III. 1983, leg. Besuchet (MHNG, cAss).

Othius microphallus spec. nov.

Holotype ♂, Teneriffa, Pico del Ingles, 27. III. 1972, leg. H. Meybohm & H. Fülscher (cAss).
Paratypes: 4 ♂♂. 4 ♀♀, same data as holotype (SMNS, cAss).

Diagnosis:
Measurements and ratios (range, n = 9): HL: 0.62–0.69; HW: 0.54–0.62; PW: 0.59–0.68; PL: 0.79–0.91; EL: 0.45–0.53; TiL: 0.48–0.56; TaL: 0.39–0.44; TL: 3.8–5.2; HL/HW: 1.10–1.16; HW/PW: 0.91–0.95; PL/PW: 1.32–1.37; EL/PL: 0.55–0.59; TiL/TaL: 1.14–1.28.

[For comparison: measurements and ratios of *O. intermedius* KORGE; range, mean (n = 31): HL: 0.69–0.88, 0.79; HW: 0.59–0.76, 0.69; PW: 0.66–0.80, 0.75; PL: 0.85–1.10, 1.01; EL: 0.48–0.65, 0.59; TiL: 0.56–0.69, 0.63; TaL: 0.44–0.56, 0.50; TL: 3.8–6.8, 5.96; HL/HW: 1.11–1.19, 0.15; HW/PW: 0.89–0.96, 0.92; PL/PW: 1.27–1.43, 1.35; EL/PL: 0.55–0.61, 0.58; TiL/TaL: 1.18–1.32, 1.25.]

In colour, punctation and proportions (see measurements) highly similar and very closely related to *O. intermedius* KORGE, from which the new species is distinguished as follows:
Size smaller (little or no overlap, see measurements, Figs 2–3).
Head with frontal punctures very deep, well-defined, and accompanied by 0–3 additional smaller punctures. (In *O. intermedius* the frontal punctures are shallower, less well-defined and usually accompanied by several [mostly 3–7] punctures.)
Microsculpture of central dorsal area of posterior half of head with predominantly long transverse and diagonal meshes (in *O. intermedius* predominantly composed of isodiametric or short transverse meshes).
♂: aedeagus in shape and internal structures similar to *O. intermedius*, but smaller [name!], 0.66–0.69 mm (*O. intermedius*: 0.74–0.77 mm); hook-shaped internal structures of different shape, slenderer and more evenly curved (Figs 1 a–d); hind margin of sternum as in *O. intermedius* (Fig. 1 e).
♀: tergum X broader and shorter than in *O. intermedius*; styli shorter, weakly projecting over hind margin of tergum X (in *O. intermedius* clearly projecting over tergum X) (Figs 1 f–g); hind margin of tergum X with modified setae.
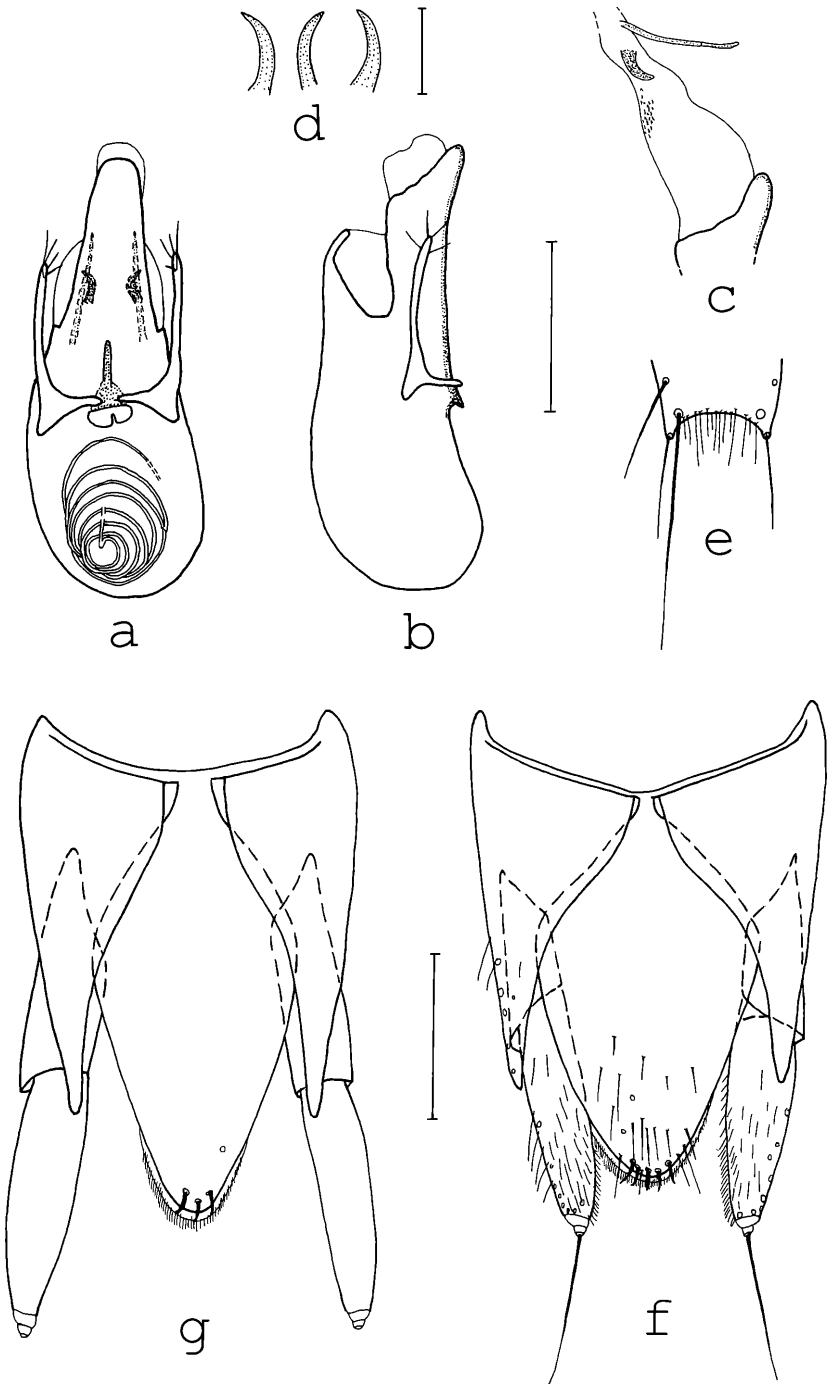
Comments:
The new species has become known only from the type locality where it was sieved in a *Laurus* wood (MEYBOHM, pers. comm.). Remarkably, *O. intermedius,* its closest relative, which is widely distributed in the Bosque de la Esperanza and adjacent areas and in the Anaga mountains, was collected near the type locality of *O. microphallus.* Further data on the distribution of the two species are needed to explain how geographical separation and eventually speciation occurred. Closely related and probably allo- or parapatric endemics with very small areas of distribution in the Anaga mountains are also known in the staphylinid genus *Oxypoda* MANNERHEIM (ZERCHE 1996).

The phylogenetics of the *Othius* species of the Atlantic Islands

With the remainder of the *Othius* species of the Western Palaearctic region recently revised and subdivided into preliminary species groups and subgroups (ASSING 1997b), a phylogenetic approach to the species of the Atlantic Islands is here attempted.
Several of the characters originally considered in the study proved to be of little value, as they were either autapomorphies of single species or subject to high intraspecific variation (e.g. the microsculpture of the head and pronotum). Most informative, on the other hand, were the micropunctation of the

Figs 1 a–g: *Othius microphallus* spec. nov. (a–f) and *O. intermedius* KORGE (g): aedeagus in ventral (a) and in lateral view (b), apex of median lobe with protruding internal sac (c), hook-shaped structures of two further ♂♂ (d), hind margin of ♂ sternum IX (e), ♀ terminalia (f, g). Scales: a–c, e–g: 0.2 mm; d: 0.05 mm.
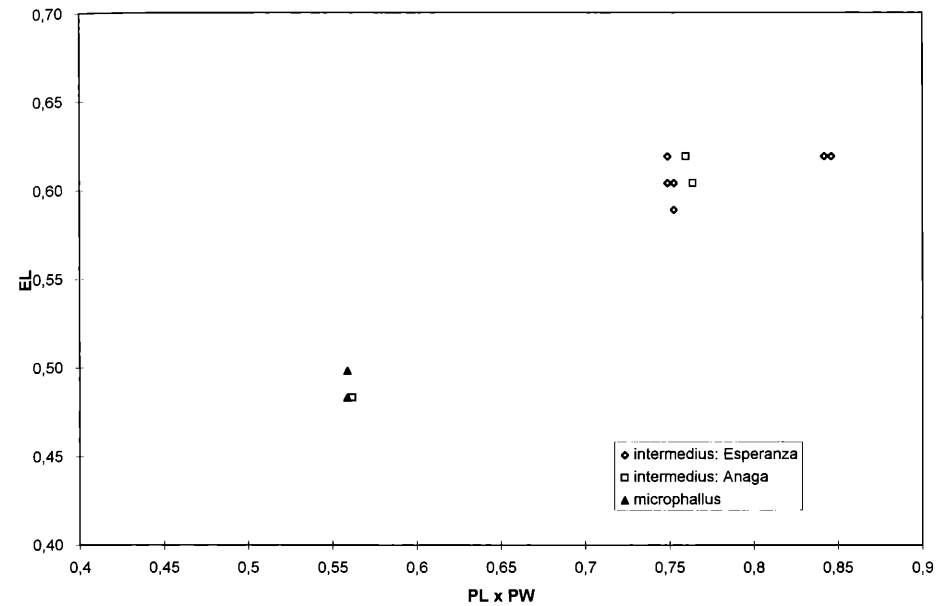
Fig. 2: Intraspecific variation of elytral length (EL) in relation to size of pronotum (PL × PW) in *Othius microphallus* spec. nov. and *O. intermedius* KORGE.
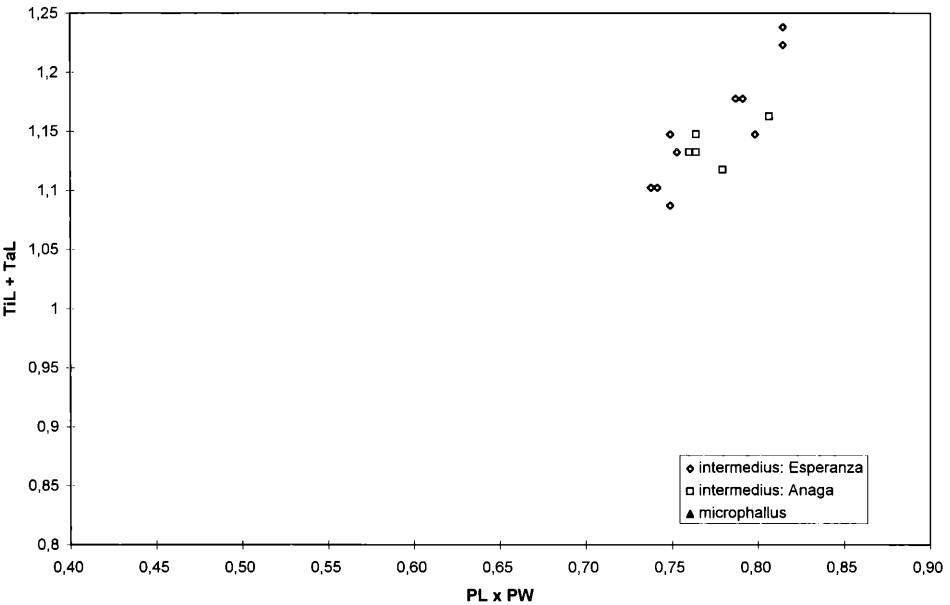
Fig. 3: Intraspecific variation of combined length of metatibia and metatarsus (TiL + TaL) in relation to size of pronotum (PL × PW) in *Othius microphallus* spec. nov. and *O. intermedius* KORGE.

forebody, the microsculpture of the elytra and especially the ♂ primary and secondary sexual characters (the shape of sternum IX and the median lobe, the presence and shape of structures in the internal sac, the number of coils and the width of the flagellum) (Tab. 1).

Character states and polarity:

1. Micropunctation of head and pronotum: absent or very indistinct (0); present (1).
2. Micropunctation of elytra: absent (0); present (1). This character is subject to some intraspecific variation and usually less pronounced in *O. jansoni*.
3. Isodiametric microsculpture of elytra: absent (0); present (1).
4. Discal punctation pattern: *subuliformis*-type (0); *laeviusculus*-type (1). In *O. punctulatus* this character is highly variable, but most specimens have (or are close to) the *subuliformis*-type.
5. Size: moderately large to large (0); small to intermediate (1). The polarity of this character is based on a preliminary examination of *Othius* from the Eastern Palaearctic region, but requires verification.
6. Eye size: large, horizontal diameter at least almost as long as, usually longer than antennomere III (0); horizontal diameter clearly shorter than antennomere III (1); the reduction of eye size has apparently evolved convergently in four groups of island species (see discussion below).
7. ♂ protarsi: strongly dilated (0); weakly dilated (1).
8. ♀ protarsi: distinctly dilated (0); weakly dilated (1).
9. Palisade fringe on hind margin of tergum VII: present (0); absent (1); for a discussion of the phylogenetic significance of this character see below.
10. ♂ hind margin of sternum VII: unmodified (0); centrally concave (1).
11. Central region of hind margin of ♂ sternum IX: at least weakly concave (0); truncate to convex (1).
12. Hind margin of ♂ sternum IX: weakly to moderately concave (0); strongly concave (1).
13. Hind margin of ♂ sternum IX: evenly concave (0); ± sinuate, undulate (1).
14. Ventral process of aedeagus: at most with short basal median carina (0); with long median carina (1) (see also discussion below).
15. Ventral process of aedeagus: apex ± U-shaped, apically rounded (0); apex ± V-shaped, apically acute (1). The acute apex of the median lobe in *O. subuliformis* is here considered a homoplast autapomorphy of that species.
16. Flagellum of internal sac of aedeagus: ± thin, 6–12 coils (0); wide and with < 5 coils or ± reduced (1).
17. Flagellum of internal sac of aedeagus: distally unmodified (0); distally widened (1); distally ± modified (2). The homology of the modified flagellum in *O. brachypterus* is indicated by the transitional condition realized in *O. microphtalmus*.
18. Flagellum of internal sac of aedeagus: distally not spear-shaped (0); distally spear-shaped (1).
19. Internal sac of aedeagus: with pair of long (mostly weakly sclerotized) structures (0); pair of long structures absent (1).
20. Internal sac of aedeagus: pair of ± triangular structures absent (0), present (1).
21. Internal sac of aedeagus: with at most one pair of long structures (0); with at least two pairs of long structures (1).
22. Internal sac of aedeagus: without pair of hook-like structures (0); with pair of hook-like structures (1).
23. Internal sac of aedeagus: without weakly sclerotized median structure (0); with long, weakly sclerotized median structure (1).
24. Dorsal face of aedeagus: normal condition, i.e. largely sclerotized (0); largely membranous (1).
25. Modified setae on ♀ tergum X: present at least in majority of specimens (0); absent (1).
26. Distribution: ± widely distributed, continental species (0); endemic to Canary Islands (1); endemic to Madeira (2).

The examination of the Atlantic species provided some evidence regarding the (previously uncertain) polarity of several characters and character states in *Othius*. The discal punctation of the pronotum is of the *O. subuliformis*-type in all Atlantic species independent of their phylogenetic affiliations, which suggests that the condition found in the European *O. laeviusculus* species group represents the apomorphic state (see ASSING 1997b). Similarly, the presence of ± long semitransparent or ± weakly sclerotized structures in the internal sac of the aedeagus appears to be plesiomorphic, as such structures were observed in at least part of the species of all groups of Atlantic *Othius*. In addition, the earlier

Table 1: Character matrix (0: plesiomorphic; 1, 2: apomorphic; L: logically impossible; D: both character states present; ?: unknown).

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
O. punctulatus	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0
O. subuliformis & O. wunderlei	0	0	0	0	1	0	0	1	D	0	0	0	0	0	D	0	0	0	0	0	0	0	0	0	1	0
O. laeviusculus	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0
O. lapidicola	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0
O. strigulosus	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	2
O. jansoni	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
O. arieiroensis	0	0	0	0	1	1	0	1	1	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	2
O. baculifer	0	0	0	0	1	1	0	1	1	1	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	2
O. ruivomontis	0	0	0	0	1	1	0	1	1	1	0	0	0	1	1	1	1	0	1	0	0	0	0	0	?	2
O. brachypterus	0	0	1	0	1	1	0	1	1	0	1	L	L	1	1	1	1	0	0	0	0	0	0	1	0	1
O. microphtalmus	0	0	1	0	1	1	0	1	1	0	1	L	L	1	1	1	1	0	0	0	0	0	0	0	0	1
O. neglectus	0	0	1	0	1	1	0	1	1	0	1	L	L	1	1	1	1	0	0	0	0	0	0	0	0	1
O. intermedius	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
O. zerchei	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
O. palmaensis	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
O. microphallus	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
O. philonthoides	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1

(Header group label spanning character columns: **Characters**)

conclusion that the absence of modified setae on the ♀ tergum X is apomorphic is confirmed a) by the presence of such setae in all Atlantic species except for *O. strigulosus* and b) by the fact that in at least two species (*O. intermedius, O. palmaensis*) ♀♀ with only one or even without any modified setae may occur.

The concept of phylogenetic relationships among Atlantic *Othius* illustrated in Fig. 4 postulates several homoplasies. Two of them (characters 6 and 9) can be explained as adaptive reductions; they are frequently encountered in soil-dwelling Staphylinidae endemic to islands. The absence of modified setae (character 25) on the ♀ tergum X has been referred to above. The absence of the pair of long structures in the internal sac (character 19) in the *O. laeviusculus* subgroup, the *O. lapidicola* subgroup (see ASSING 1997b) and *O. baculifer/ruivomontis* conflicts with various other characters; it is most parsimoniously explained as a convergent reduction. The question whether the species of the *O. lapidicola* subgroup are more related to both the Madeiran *O. arieiroensis* subgroup and the Canarian *O. brachypterus* subgroup (supported by characters 14, 15), or to the *O. laeviusculus* subgroup (supported by characters 4, 19), is not easily answered. However, in view of the intraspecific variability of the pronotal punctation (character 4) in *O. lapidicola* and the – supposedly convergent (see above) – absence of long internal structures (character 19) also in species of the *O. arieiroensis* subgroup, the former hypothesis is here favoured. The similarities in the morphology of the ventral process (characters 14, 15) in *O. punctulatus* on the one hand and in *O. lapidicola* and related subgroups on the other is very unlikely to be homologous, as this would conflict with numerous other characters. For a discussion of the distribution (character 26) see below.

As shown in the dendrogram, further clarification is required regarding the relationships at the higher species group level. One of the major problems in the phylogenetic concept is the absence of clear apomorphies constituting the *O. subuliformis* species group. Characters previously considered apomorphic, especially the presence of long semitransparent structures, seem to be plesiomorphic in fact. Another difficulty lies in the fact that it was not possible to identify an obvious sister group of *O. strigulosus* and *O. jansoni,* which is one reason why the relationship between these species and *O. punctulatus* as suggested in Fig. 4 can only be considered tentative.
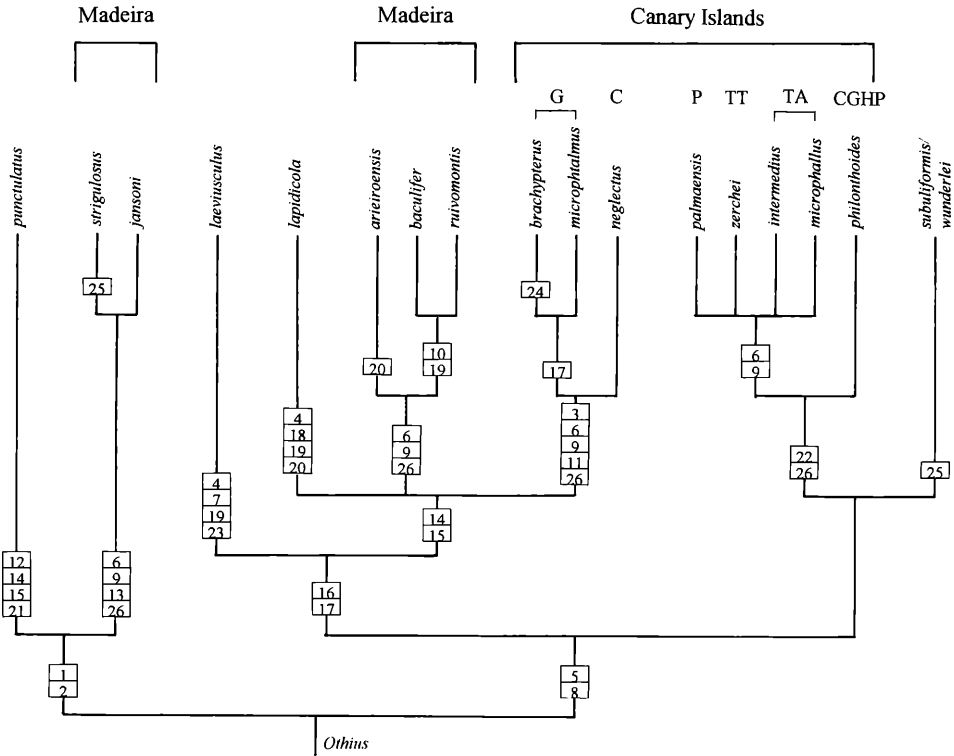
Fig. 4: Phylogeny of Atlantic *Othius*. C: Gran Canaria; G: La Gomera; H: Hierro; P: La Palma; TT: Tenerife, Teno; TA: Tenerife, Anaga.

A major weakness of the phylogenetic approach here attempted is obviously the fact that a suitable out-group has not yet been identified. Many species of *Othius* from the Eastern Palaearctic and further zoo-geographical regions have not yet been fully revised. Moreover, a phylogenetic study of other Othiini is required in order to determine the sister group of *Othius* and thus assess the – currently uncertain – polarity of several character states. On the other hand, the results of the phylogenetic analysis at the species (sub-)group level presented here are believed to be sufficiently firm to support the conclusions in the following section.

Colonization of the Atlantic Islands

According to BAEZ (1993), Madeira proper has existed for approximately 3 million years, during which time colonization must have taken place. The larger Canarian Islands are estimated to be between 0,6 and ca. 35 million years old (see ZERCHE 1996 for a comparison and discussion of various estimates). Little is known regarding the colonization of the Atlantic Islands by Staphylinidae. In Canarian *Oxypoda* MANNERHEIM, eight independent colonization events can be assumed. Five of them are – except for *O. lurida* WOLLASTON – more recent introductions of widespread species; three of them occurred early enough to lead to subsequent speciation. 18 endemic species of *Oxypoda* in three subgenera (one of them endemic) are known from the Canary Islands (ZERCHE 1996 and pers. comm.).

The genus *Othius* STEPHENS is represented in Madeira by five and in the Canary Islands by eight ende-mic species, figures which among other staphylinid genera are only equalled or exceeded by *Geostiba*

THOMSON, *Stenus* LATREILLE and possibly *Atheta* THOMSON (Madeira), and by *Oxypoda* MANNER-HEIM, *Stenus* (subspecies included), *Metopsia* WOLLASTON, *Astenus* STEPHENS and *Atheta* (Canary Islands), respectively (ASSING & WUNDERLE 1994, 1996; HERNANDEZ et al. 1994; ISRAELSON 1971; ZERCHE 1996, 1998). As can be concluded from the phylogenetic analysis above (Fig. 4), both the Madeiran and the Canarian archipelago were apparently successfully colonized twice by species of *Othius*, not counting the recent introduction of *O. punctulatus* to the Canary Islands.

The common continental ancestor of the 5 species of the *O. intermedius* subgroup (*O. intermedius, O. microphallus, O. zerchei, O. palmaensis,* and *O. philonthoides*) seem to have come from the Western Mediterranean, and is likely to have reached the Canary Islands in more recent (geological) times; the nearest continental relatives (*O. subuliformis* STEPHENS, *O. wunderlei* ASSING) today occur in the Iberian Peninsula. In the *O. intermedius* subgroup, speciation has led to only little character divergence; the polytomy in Fig. 4 is a result of the lack of workable characters. Adaptive reductions (wings, palisade fringe, eyes), apparently directly or indirectly resulting from the selective pressure against flying, are less pronounced than in other groups of island endemics in *Othius*. One of the species may still be capable of flight (ASSING 1997a). Three of the species occur in Tenerife, with one of them (*O. zerchei*) confined to the Teno mountain range, one species (*O. microphallus*) to the Anaga mountain range, and the distribution of *O. intermedius* extending from the Anaga mountains to the northeastern parts of the central mountain ranges (Bosque de la Esperanza and adjacent areas). This pattern of distribution, especially the geographic isolation of *O. zerchei,* would suggest that speciation and consequently also colonization occurred before the fusion of Anaga and Teno, which according to MAYER & BISCHOFF (1991) took place in the Quaternary.

The more pronounced character divergence and reductions as well as the greater number of apomorphies in the *O. brachypterus* and the *O. arieiroensis* subgroup indicate that a longer period of evolutionary time has passed since their ancestors colonized the Canary Islands and Madeira, respectively. Their ancestors are likely to have come from either the Iberian Peninsula or Northwest Africa, independent of whether both subgroups originated from an ancestor of the *O. lapidicola* subgroup or that of the whole *O. laeviusculus* group. No character was found suggesting a closer relationship between the *O. lapidicola* subgroup and either of the *O. brachypterus* and the *O. arieiroensis* subgroup; hence the polytomy in Fig. 4. If the conclusions drawn in the phylogenetic analysis are true, the nearest relative in the Western Mediterranean is *O. piceus* SCRIBA. Characters 6 and 9, which are shared by both the *O. brachypterus* and the *O. arieiroensis* subgroup, are adaptive reductions of the palisade fringe and eye size, which are practically certain to have – independently – occurred after the colonization; the islands are highly unlikely to have been reached by specimens which were incapable of flight. In addition, the probability of colonization from the continent is obviously clearly higher, not only because of the lower selective pressure against flight, but also because of the much larger populations.

There is some evidence that a volcanic eruption devastated La Gomera, which is inhabited by two of the three species of the phylogenetically older *O. brachypterus* subgroup, ca. 2 million years ago and that the island was completely recolonized afterwards (ZERCHE 1996). If this is true, the ancestor(s) may not have reached the island before the Quaternary. The age of Gran Canaria, which is inhabited by the third species of the *O. brachypterus* subgroup (*O. neglectus*) is estimated to be approximately 14 million years. In view of this island's higher age, larger size and lower distance from Africa and Europe as well as the more primitive morphology of the aedeagus in *O. neglectus,* Gran Canaria may well have been the first island to be colonized by the ancestor of the *O. brachypterus* subgroup. A comparison with character divergence in other Atlantic *Othius* groups, however, suggests that colonization of this island did not take place until the last few million years. No species of *Othius* are known from the eastern Islands Lanzarote and Fuerteventura, whose age estimates range from 19 to 38 million years, but the possibility that they were once colonized by *Othius*, which disappeared together with the *Laurus* woods, cannot be ruled out.

The systematic position of the *O. strigulosus* group (*O. strigulosus, O. jansoni*) is somewhat isolated, which suggests that this group is phylogenetically rather old. As pointed out above, there are some doubts regarding its affiliations to the *O. punctulatus* group; therefore, it is here treated as a group of its own rather than a subgroup of the *O. punctulatus* group. Although it is certain that the ancestor of

the *O. strigulosus* group colonized Madeira independently of and probably before the ancestor of the *O. arieiroensis* subgroup, its origin is not clear. Practically all of the original Mediterranean laurel woods have vanished, and closely related continental species have apparently gone extinct. If this is true, the ancestor of the *O. strigulosus* group arrived in Madeira at a time, when the Laurisilva was still widely distributed in the Mediterranean.

Zusammenfassung

Weitere Nachweise auf Madeira und den Kanarischen Inseln verbreiteter *Othius*-Arten werden vorgelegt. *Othius coiffaiti* LOHSE und sein Synonym *O. pseudolapidicola* COIFFAIT werden mit *O. philonthoides* WOLLASTON synonymisiert. *O. microphallus* spec. nov. (Teneriffa) wird beschrieben und mit dem naheverwandten *O. intermedius* KORGE verglichen; die primären und sekundären Sexualmerkmale werden abgebildet. Eine phylogenetische Analyse der *Othius*-Arten der Atlantischen Inseln zeigt, daß die Gattung auf Madeira und den Kanaren mit jeweils zwei monophyletischen Gruppen vertreten ist und somit für beide Inselgruppen jeweils zwei erfolgreiche Besiedlungsereignisse durch *Othius*-Arten anzunehmen sind. Die Kanarischen Inseln wurden darüber hinaus offenbar erst in jüngster Vergangenheit durch *O. punctulatus* (GOEZE) besiedelt. Die Phylogenie der atlantischen *Othius*-Arten und die Besiedlung der Inseln werden diskutiert.

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