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Pill-millipedes of the Canary Islands: the *Glomeris alluaudi*-group (Diplopoda, Glomeridae)

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ABSTRACT: The apparently monophyletic *Glomeris alluaudi*-group comprises six species, all endemic on the Canary Islands: *G. alluaudi* Brölemann, 1901 (Tenerife), *G. speobia* n. sp. (Tenerife, cave dweller), *G. gomerana* Attems, 1911 (La Gomera), *G. canariensis* Golovatch, 1987 (La Gomera), *G. vicentean* sp. (Gran Canaria), and *G. hierroensis* n. sp. (El Hierro). An additional unidentified member of this group, apparently epigean, occurs on La Palma. A key is provided to all of the described forms, and distribution, variation and some evolutionary aspects are discussed.

Key words: Diplopoda, *Glomeris*, Canary Islands.

RESUMEN: El grupo aparentemente monofilético de *Glomeris alluaudi* comprende seis especies, todas endémicas de Canarias: *G. alluaudi* Brölemann, 1901 (Tenerife), *G. speobia* n. sp. (Tenerife, cavernícola), *G. gomerana* Attems, 1911 (La Gomera), *G. canariensis* Golovatch, 1987 (La Gomera), *G. vicentean* sp. (Gran Canaria), y *G. hierroensis* n. sp. (El Hierro). Otro miembro no identificado de este grupo, al parecer epigeo, se encuentra en La Palma. Se aporta una clave de identificación para todas las formas descritas, y se discute su distribución, variación y algunos aspectos evolutivos.

Palabras clave: Diplopoda, *Glomeris*, islas Canarias.

INTRODUCTION

As mentioned in a recent review of the millipedes of the Canary Islands (Vicente & Enghoff, 1999), the prolific Euro-Mediterranean genus *Glomeris* Latreille, 1802/03 is represented on these islands by three described and a few unidentified species, including at least one apparent cave-dweller from Tenerife. The hitherto described species are from

Tenerife (*G. alluaudi* Brölemann, 1901) and La Gomera (*G. gomerana* Attems, 1911 and *G. canariensis* Golovatch, 1987), while the records of *Glomeris* from Gran Canaria and El Hierro have so far remained unidentified to species (Vicente & Enghoff, 1999).

The present paper is an up-to-date review of the fauna and distribution of *Glomeris* in the Canary Islands, with some evolutionary, biogeographical and ecological considerations.

MATERIAL AND METHODS

Our deceased colleague Maria Cristina Vicente (Barcelona) started but never completed a revision of Canarian *Glomeris*. Much of the material studied by Cristina Vicente was donated by her to the Zoological Museum, University of Copenhagen. In addition, a large collection of specimens, mainly from Teneriffan caves, collected by the “Grupo de Investigaciones Espeleológicas de Tenerife, Universidad de la Laguna”, was kindly put at our disposal by Pedro Oromí, Universidad de La Laguna, Tenerife. Together with material already present in the Zoological Museum, Copenhagen these two collections form the basis for the present contribution.

For systematic-phylogenetic considerations we studied several species of *Glomeris* as well as representatives of a few other glomerid genera in the Copenhagen collection. In particular, measurements etc. were taken on *Glomeris marginata* (Villers, 1789), *G. pulchra* C.L. Koch, 1847, *G. albidonigra* Strasser, 1977, *Hyleoglomeris cremea* Golovatch, 1983, *H. lenkorana* Golovatch, 1976, and *Loboglomeris pyrenaica* (Latzel, 1886). A proper phylogenetic analysis has, however, not been carried out and would require much additional study.

Selected specimens were studied with a JEOL JSM 840 Scanning Electron Microscope.

Acronyms of repositories are given in Table I.

Table I. Abbreviations used in the text:

DZUL	Departamento de Zoología, Universidad de La Laguna, Tenerife
GIET	Grupo de Investigaciones Espeleológicas de Tenerife, Universidad de la Laguna
MCNT	Museo de Ciencias Naturales de Tenerife
MSS	Mesocavernous shallow stratum (= Milieu souterrain superficiel)
ZMUC	Zoological Museum, University of Copenhagen
ZMUM	Zoological Museum, Moscow

THE *GLOMERIS* *ALLUAUDI*-GROUP

The *Glomeris* species of the Canary Islands form the westernmost outpost in the distribution of the entire genus which is represented by numerous (> 50) species throughout the west Palaearctic continental area.

The Canarian *Glomeris* species have long been recognized as constituting a distinct species group. It was formalized as *Trichoglomeris* Verhoeff, 1906, first treated as a full-

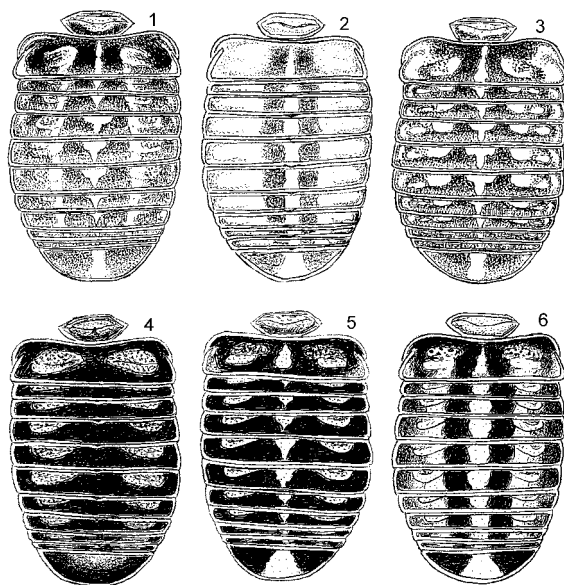
rank genus, later as a subgenus of *Glomeris*, but recently (Golovatch, 1987) downgraded to an informal category, the *alluaudi*-group, with the following combination of characters: (1) micropilosity of the terga (Figs. 29, 31); (2) unusually long and slender antennae; (3) outer coxal lobes of the male leg 17 unusually high (rather reminding of *Hyleoglomeris* Verhoeff, 1910); (4) Tömosvary's organ almost transverse (Figs. 36-37); and (5) caudofemoral process of male leg 19 (telopods) varying from typically *Glomeris*-like to almost *Hyleoglomeris*-like (differentiated) (Golovatch, 1987). Whereas monophyly of the group seems well substantiated, the position of the *alluaudi*-group within the large genus *Glomeris* has not been established, and until this happens, we prefer not to use a subgeneric name for the group although one is available.

TAXONOMY

Glomeris alluaudi Brölemann, 1901

Figs. 1, 2, 7-9, 17.

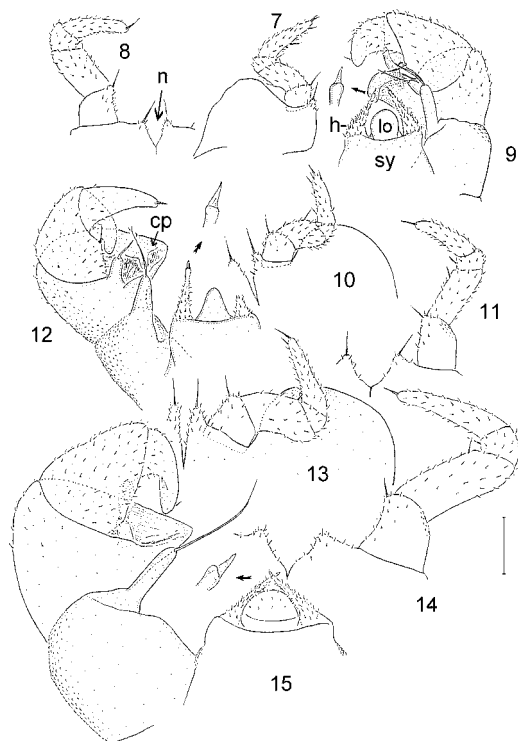
Material (all from TENERIFE): 10 ♂, 9 ♀ (ZMUC), 1 ♂, 1 ♀ (ZMUM), 1 ♂ (DZUL) Volcán Negro, 6.ix.1989, leg. R. Rodríguez. – 1 ♀ (ZMUC) Alto de las Casillas, 6.ii.1989, leg. R. Rodríguez. – 2 ♀ (DZUL), Las Lagunetas, 29.i.1993 leg. P. Oromí.. – 1 ♂, 2 ♀ (DZUL) Fuente Joco, 27.xii.1996, leg. P. Oromí.



Figs. 1-6. Colour patterns. – 1-2: *Glomeris alluaudi* (1: Orotava, 2: Volcán Negro). – 3: *G. gomerana*. – 4: *G. vicentae* n.sp., holotype. – 5-6: *G. hierroensis* n.sp., ♂ paratypes. (Figs. 1 & 3 after Golovatch 1987). – (not to scale.)

Diagnosis: Distinguished by small size and a clear colour pattern comprising, i.a., an axial stripe or series of spots. Differs from the similar *G. hierroensis* (El Hierro) by sinuate tergal hind margins, from the similar *G. gomerana* (La Gomera) by angulate caudofemoral process of telopods. Differs from the coninsular troglobiont *G. speobia* by the generally smaller body size, the persisting colour pattern, and the shorter antennae.

Descriptive remarks: One of the smallest species in the group, body length 4.0-5.5 (♂) / 4.1-6.4 mm (♀), width 2.1-3.0 (♂) / 2.2-3.5 mm (♀). Antennomere 6 2.4-2.7 times as long as wide. Colour pattern slightly variable, usually



Figs. 7-15. ♂ legs 17 (7, 10 & 13), 18 (8, 11 & 14), and 19 (9, 12 & 15) in *Glomeris alluaudi* (7-9), *G. gomerana* (10-12), and *G. canariensis* (13-15). – Scale 0.2 mm. (After Golovatch 1987). – cp: caudofemoral process, h: syncoxital horn, lo: syncoxital lobe, n: syncoxital notch, sy: syncoxite.

quite vivid (Fig. 1) but often paler, with lateral parts of terga 2-10 almost entirely pallid, and pygidium with a broader central, subtrapeziform spot (Fig. 2). Male leg 17 (Fig. 7) with outer coxal lobe rather high, somewhat variable in shape. Male leg 18 (Fig. 8) normal, syncoxital notch can be broader than shown. Male legpair 19 (= telopods) (Figs. 9 & 17) with a roundish to linguiform syncoxital lobe, prefemur and femur or only prefemur very finely papillate; caudofemoral process invariably slightly but distinctly angulate at base.

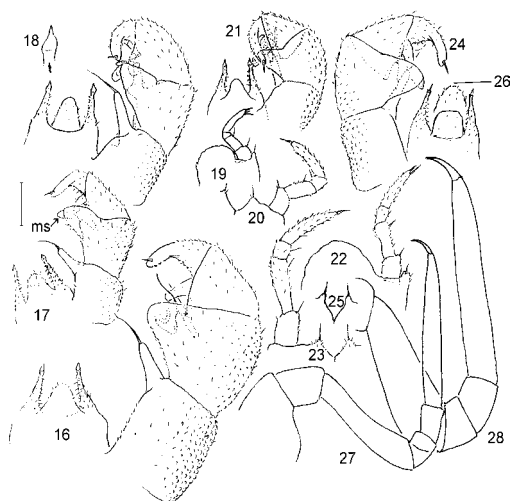
***Glomeris speobia* n.sp.**

Figs. 22-24, 27, 33, 36, 39.

Material (all from TENERIFE): *Holotype* ♂ (DZUL), Canary Islands, Tenerife, Cueva de Felipe Reventón, 11.v.1999, leg. GIET. – *Paratypes*: 3 ♀ (DZUL), same data, together with holotype. – 1 ♀ (ZMUC), same locality, 6.v.1999, leg. GIET. – 1 ♂, 2 ♀ (DZUL), 1 ♀ (ZMUM), same locality, 12.i.2000, leg. GIET. – 2 ♂ (ZMUM) Cueva de los Roques, 25.iv.1999, leg. GIET. – 2 ♂, 1 ♀ (MCNT), 2 ♂ (ZMUC), same locality, 23.x.1999, leg. GIET. – 1 ♂ (DZUL), Cueva de Chío, 30.vi.1999, leg. GIET. – 1 ♀ (DZUL), same locality, 30.xi.1999, leg. GIET. – 2 ♂ (DZUL), Cueva del Sobrado SVP (H. Pacheco), 31.x.1999, leg. GIET. – 1 ♂ (DZUL), Cueva Fea de Arico, 2.xi.1999, leg. GIET. – 1 ♂ (DZUL), Cueva de la Labrada, 5.vi.1999, leg. GIET. – 1 ♀ (DZUL), same locality, 28.iii.1992, leg. P. Oromí. – 2 ♀ (DZUL) Cueva de la Chatarra, 23.x.1991, leg. P. Oromí. – 1 ♂ (DZUL), same locality, 23.x.1991, leg. J. L. Martín. – 3 ♂, 1 ♀ (DZUL), Cueva de los Roques, Parque Nacional del Teide, Las Cañadas, 24.xi.1999, leg. P. Oromí.

The specific name refers to the cave-dwelling habits of the species.

Diagnosis: Differs from congeners by the virtually depigmented cuticle coupled with a caudally slightly protruding hyposchism, and slightly slenderer legs. Differs especially from the coninsular *G. alluaudi* by the larger body size.



Figs. 16-28. ♂ legs 16 (27-28), 17 (19, 22), 18 (20, 23, plus 25 as variation of syncoxital notch), and 19 (16-18, 21, 24 plus 26 as variation of syncoxital lobe) in *Glomeris canariensis* Golovatch, 1987 (16, 28: Bosque del Cedro), *G. alluaudi* (17: Volcán Negro), *G. vicenteae* n.sp. (18, holotype), *G. hierroensis* n.sp. (19-21, ♂ paratype), *G. speobia* n.sp. (22-24, 27, ♂ paratype, Cueva Sobrado; 25, ♂ paratype, Cueva de Felipe Reventón; 26, ♂ paratype, Cueva de los Roques). – Scale 0.2 mm. – ms: membranous sac on caudofemoral process.

Legs particularly slender (Fig. 27), when stretched in situ slightly surpassing lateral edge of respective tergum. Male leg 17 with a very high, somewhat irregularly shaped outer coxal lobe (Fig. 22). Syncoxital notch of male leg 18 broad to rather narrow, slightly varying in shape from subtriangular to gothic arch (Figs. 23 & 25). Male legs 19 (= telopods, Fig. 24) with a large, subtrapeziform to (sub)linguiform syncoxital lobe (Figs. 24 & 26); lateral horns of syncoxite rather slender, setose, apically with an acuminate lappet; lateral surfaces of prefemur and, at least subbasally, femur micropapillate; caudofemoral process very prominent, not angulate at base, with a distinct membranous sac distally; tarsus narrowly rounded at tip.

Remarks: See the section “Cave glomerids” and “Addendum”.

Glomeris gomerana Attems, 1911

Figs. 3, 10-12.

Material (all from LA GOMERA): 2 ♂ (ZMUC), Bosque del Cedro, near Montaña de la Asomada N La Laguna Grande, 1180 m, laurisilva, under stone, 6.ii.1989, leg. H. Enghoff. – 1 ♂, 1 ♀ (ZMUC), pine forest, 1200 m, x-xi.1978, leg. J. Rabøl, – 1 ♂ (ZMUC), Alto Garajonay, 1400 m, *Pinus canariensis* plantation with *Erica* & *Adenocarpus*, under

Description: One of the largest species in the group, body length 6.5-8.0 (♂) / 5.6-9.0 mm (♀), width 3.0-4.3 mm (♂, ♀). Holotype ca. 7.4 mm long and 3.8 mm wide. Body cuticle entirely depigmented, distal parts of tarsi and/or lateralmost parts of terga rarely slightly yellowish.

Ocelli reduced, never black, sometimes individual ocelli discernible as darker, pale brownish spots, at least 6+1 in number. Antennae elongate, quite slender, antennomere 6 (Fig. 33) 2.8-3.0 times longer than wide. Tömösvary's organ (Fig. 36) particularly large and elongate, 3.0-3.5 times longer than broad. Collum with two transverse striae. Thoracic shield with 0-2 striae, when present beginning anteriorly of or at schism, one or both crossing entire dorsum. Hyposchism particularly small and narrow, regularly rounded, slightly surpassing rear tergal contour (Fig. 39). Hind edge of terga slightly but clearly sinuate in middle. Tergal surface very finely and densely pilose. Pygidium regularly convex, regularly rounded at caudal edge.

stone, 8.ii.1989, leg. H. Enghoff. – 1 ♂ (ZMUM), Base del Garajonay, 22.iii.1989, leg. R. Rodríguez. – 1 ♂, 2 ♀ (ZMUC) Laguna Grande, 22.iii.1989, leg. R. Rodríguez. – 1 ♀ (ZMUC), 2 ♂ juv. (ZMUC), El Cedro, 22.iii.1989, leg. R. Rodríguez. – 2 ♂ (DZUL) Los Acebiños, 20.ix.2002, leg. P. Oromí, – 1 ♂ (ZMUM), Alto de Garajonay, 1300 m, 17.iv.2003, leg. & ded. W. Schawaller, – 3♂, 1♀ (ZMUM), SW of La Laguna Grande, 1100 m, 21.iv.2003, leg. & ded. W. Schawaller. – Part of this material has already been published (Golovatch, 1987; Vicente & Enghoff, 1999).

Diagnosis: Distinguished by a clear colour pattern comprising, i.a., an axial stripe or series of spots. Differs from the similar *G. hierroensis* (El Hierro) by sinuate tergal hind margins, from the similar *G. alluaudi* (Tenerife) by non-angulate caudofemoral process of telopods. Differs from the coninsular and often syntopic *G. canariensis* easily by the generally smaller body size and the presence of an axial series of pale spots on the dorsum.

Descriptive remarks: Medium-sized, body length 4.2-6.0 (♂) / 4.3-9.0 mm (♀), width up to 3.4-3.9 (♂) / 3.5-5.1 mm (♀). Antennomere 6 2.6-3.2 times as long as wide. Colour pattern basically as in Fig. 3, slightly variable, sometimes anterolateral parts of thoracic shield not as broadly pallid as is typically the case, thus slightly reminding of the condition in typical *G. alluaudi* (cp. Fig. 2). Male leg 17 (Fig. 10) with outer coxal lobe high, somewhat variable in shape. Male leg 18 (Fig. 11) normal, syncoxital notch can be somewhat narrower than shown. Male legs 19 (= telopods, Figs. 12) with a roundish to linguiform syncoxital lobe, both prefemur and femur very finely papillate; caudofemoral process invariably non-angulate at base but apical membranous sac prominent.

***Glomeris canariensis* Golovatch, 1987**

Figs. 13-15, 16, 28, 31, 34, 37, 40.

Material (all from LA GOMERA): 1 ♂, 3 ♀, 1 juv. (ZMUC) Bosque del Cedro, near Montaña de la Asomada N La Laguna Grande, 1180 m, laurisilva, under bark of relatively dry log, 6.ii.1989, leg. H. Enghoff. – 1 ♂ (ZMUC), same locality, in small moist log, 6.ii.1989, leg. H. Enghoff. – 1 ♀ (ZMUC), same locality in log, 6.ii.1989, leg. H. Enghoff. – 1 ♂ (ZMUC), same locality, under stone, 6.ii.1989, leg. H. Enghoff. – 1 ♂ (ZMUC) Las Mimbrenas near Eta. N.S. de Lourdes, 950 m, laurisilva at stream, in log, 8.ii.1989, leg. H. Enghoff. – 1 ♀ (ZMUC), same locality, in small rotten log, 8.ii.1989, leg. H. Enghoff. – 1 ♂, 1 ♀ (ZMUC) 1-2 km SSW La Cerpa, 950-1000 m, laurisilva, in log, 9.ii.1989, leg. H. Enghoff. – 1 ♂ (ZMUC), same locality, under bark of dead tree, 1.5 m above ground, 9.ii.1989, leg. H. Enghoff. – 5 ♂, 2 ♀ (ZMUC), same locality, 1000-1040 m, in/under small log, 6.ii.1989, leg. H. Enghoff. – 1 ♂ (ZMUC), near Los Acebiños, 900 m, laurisilva, under bark of log, 8.ii.1989, leg. H. Enghoff. – 1 ♂ (ZMUC), same locality, in log, 8.02.1989, leg. H. Enghoff. – 1 ♂, 3 ♀ (ZMUC), same locality, 20.ix.2002, leg. P. Oromí. 4 ♂, 4 ♀ (ZMUC), El Cedro, in rotten logs, 24.iii.1988, leg. A Fjellberg. – 2 ♂, 8 ♀, 2 ♀ juv. (ZMUC), 1 ♂ (DZUL), 1 ♂ (ZMUM), same locality, 22.iii.1989, leg. R. Rodríguez. – 1 ♀ (DZUL), same locality, 21.iii.1989, leg. R. Rodríguez. – 1 ♂ (DZUL), same locality, 26.xii.1987, leg. P. Oromí. – 1 ♂, 1 ♀ (DZUL), same locality, 28.iv.1995, leg. P. Oromí. – 1

♀ (DZUL), same locality, 17.v.1996, leg. P. Oromí. – 1 ♂ (DZUL), Reventón Oscuro, MSS, 3.i.2003, leg. P. Oromí & H. Contreras. – 4 ♀, 2 juv. (DZUL), same locality, MSS, 11.v.2003, leg. P. Oromí. – 1 ♂, 1 ♀ (DZUL), same locality, 19.ii.2003, leg. A.J. Pérez, – 1 ♂ (ZMUM), El Cedro, 900 m, 15-24.iv.2003, leg. & ded. W. Schawaller. – Part of this material has already been published (Vicente & Enghoff, 1999).

Diagnosis: Distinguished by large size, a very indistinct to absent colour pattern and lack of an axial stripe or series of spots. Differs from the superficially more similar species, *G. vicenteae* (Gran Canaria) by the poorly developed membranous sac at tip of caudofemoral process of telopods. Differs from the coninsular and often syntopic *G. gomerana* easily by the generally larger body size and the lack of an axial series of pale spots on the dorsum.

Descriptive remarks: The largest species in the group, body length 5.2-11.5 (♂) / 5.4-13.4 mm (♀), width 3.9-6.0 (♂) / 4.0-6.4 mm (♀). Antennomere 6 2.6-3.0 times as long as wide. Colour pattern somewhat variable, vague sublateral spots on terga sometimes traceable as well as a slightly paler base of pygidium, i.e. a pattern close to that of *G. vicenteae* (Fig. 4). A very vague, thin, paler, axial line very seldom discernible on terga in addition to vague sublateral spots, this line continuing onto pygidium (♀, 13.4 mm long, 6.4 mm wide). Some particularly small individuals (♂, 6.3 mm long, 3.9 mm wide) pale brownish yellow, with pattern only discernible through transverse darker bands in rear halves of terga 1-10, head and pygidium almost pallid. Venter almost invariably very dark. Legs rather stout (Fig. 28). Male leg 17 (Fig. 13) with outer coxal lobe somewhat variable in shape but always high. Male leg 18 (Fig. 14) also normal, syncoxital notch can be somewhat narrower than shown. Male legs 19 (= telopods) (Figs. 15 & 16) with a roundish to linguiform syncoxital lobe, both prefemur and femur or only prefemur very finely papillate; caudofemoral process invariably non-angulate at base, apical membranous sac poorly developed or absent.

***Glomeris vicenteae* n.sp.**

Figs. 4, 18.

Material: *Holotype* ♂ (ZMUC), Canary Islands, Gran Canaria, Barranco de Guayadeque, 700-800 m, 27.xii.1985, leg. R. Rodríguez. – *Paratype* ♀ (ZMUC), same data, together with holotype. – 1 ♂ (DZUL), Majaletes-Cazadoes, traps in MSS, 13.iv.2003, leg. H. López.

The specific name honours and commemorates the late Dr. Maria Cristina Vicente, Barcelona, Spain.

Diagnosis: Distinguished by rather large size, a relatively indistinct colour pattern lacking an axial stripe or series of spots but with quite distinct, sublateral, marbled, paler spots on terga 2-10. Differs from the superficially more similar species, *G. canariensis* (La Gomera) by the well-developed membranous sac at tip of caudofemoral process of telopods.

Description: Body length 6.0 (♂) to 6.5 mm (♀), width 3.4 (♂) to 3.7 mm (♀). Colour of dorsal side brown (♂) to dark brown (♀) with yellowish, usually marbled markings, pattern as in Fig. 4; venter, legs and tip of antennae pallid, only distal podomeres slightly brownish. Collum usual, with a central paler spot. Thoracic shield to tergum 10 each with a pair of large, marbled, paler, subtransverse-oval spots distinctly separated not only medially but also well removed from lateral edges of terga (Fig. 4). Pygidium without distinct markings, only its mediobasal part somewhat paler than remaining parts.

Ocelli black, 7+1 (♂) / 6+1 (♀) on each side of head. Antennae elongate, slender, antennomere 6 2.8-3.0 times longer than wide. Tömösvary's organ large but of normal shape, subtransverse-oval in shape. Collum with two transverse striae. Thoracic shield with three (♂) / four (♀) striae, nearly all beginning near/beneath schism and generally poorly discernible; two (♂) / three (♀) striae crossing entire dorsum. Hyposchism rather small and narrow, regularly rounded, reaching the rear tergal contour but not protruding caudad beyond it. Most terga slightly sinuate at hind edge middorsally. Tergal surface very finely and densely pilose. Pygidium regularly convex and regularly rounded at caudal edge.

Legs rather long and slender, when stretched in situ slightly surpassing lateral edge of respective tergum. Male legs 17 and 18 lost during dissection. Male legs 19 (= telopods, Fig. 18) with a large, linguiform, nearly bare syncoxital lobe; lateral horns of syncoxite rather slender, setose, apically with an acuminate lappet; lateral surface of prefemur micropapillate; caudofemoral process very prominent, very poorly but evidently angulate at base, with a distinct membranous sac distally; tarsus narrowly rounded at tip.

***Glomeris hierroensis* n.sp.**

Figs. 5, 6, 19-21, 29.

Material (all from El Hierro): *Holotype* ♂ (ZMUC), Canary Islands, Hierro, El Brezal, iii.1989, leg. R. Rodríguez. – *Paratypes*: 8 ♂, 2 ♀, 2 juv. (ZMUC), 1 ♂, 1 ♀ (MCNT), 2 ♂, 2 ♀ (ZMUM), same data, together with holotype. – 3 ♂, 4 ♀ (ZMUC), same locality, 2.iv.1989, leg. R. Rodríguez. – 7 ♂, 31 ♀, 1 ♀ juv. (ZMUC), same locality, El Fayal, fayal-brezal, 1300 m, 31.iii.1989, leg. R. Rodríguez. – 1 ♀ (ZMUC), same locality, 300 m, 31.03.1989; leg. M. C. Vicente. – 2 ♂, 1 ♀ (DZUL), El Fayal, 4.ii.1997, leg. P. Oromí. – 1 ♀ (DZUL), same locality, 30.iii.2000; leg. P. Oromí. – 1 ♂, 1 ♀ (DZUL), Mancafete, 2.xi.2001, leg. H. Contreras.

The specific name refers to the type locality.

Diagnosis: Distinguished by small size and a clear colour pattern comprising, i.a., an axial stripe or series of spots. Differs from the similar *G. alluaudi* (Tenerife) and *G. gomerana* (La Gomera) by non-sinuate tergal hind margins.

Description: One of the smallest species in the group, body length 2.8-4.1 (♂) / 3.9-6.2 mm (♀), width 1.5-2.4 (♂) / 2.0-3.3 mm (♀). Holotype ca. 4.1 mm long and 2.4 mm wide. Colour of dorsal side normally brown to dark brown-blackish with yellowish, usually marbled markings, pattern as in Figs. 5 & 6, venter, legs and tip of antennae pallid, only distal podomeres slightly brownish. Overall impression occasionally pale rather than

dark due to hypertrophied markings. Collum with a central paler spot. Thoracic shield to tergum 10 each with a more or less rounded, axial, pale spot and a pair of large, marbled, paler, subtransverse-oval spots distinctly separated not only medially but also well removed from lateral edges of terga (Fig. 6); axial spots usually narrowed abruptly caudad; sublateral spots quite often (especially in smaller individuals, i.e., mostly males and juveniles) forming a paramedian pair of more or less continuous, pale stripes (Fig. 6, same in holotype); each sublateral spot occasionally broken into two, thus dorsum with five longitudinal rows of pale spots. Axial spot on thoracic shield invariably elongated, usually club-shaped, caudolateral corner of shield normally a little paler than background (Figs. 5 & 6), much of to virtually entire lateral part rarely pallid (much like typical *G. gomerana*) or nearly completely dark (much like *G. canariensis*). Pygidium with a distinct, subtrapeziform, pale, axial spot broadening caudad, this spot being usually broader in smaller/younger individuals than in larger specimens.

Ocelli black, 6+1 (usually in smaller individuals), 7+1 or, normally, 8+1 in larger specimens. Antennae elongate, slender, antennomere 6 2.5-2.7 times longer than wide. Tömösvary's organ large but of usual shape, subtransverse-oval in shape. Collum with two transverse striae. Thoracic shield with 3-4 striae, nearly all beginning near/beneath schism and generally poorly discernible, two striae crossing entire dorsum. Hyposchism rather small and narrow, rounded regularly, reaching to almost reaching rear tergal contour but never protruding caudad beyond it. Terga virtually not sinuate at hind edge middorsally. Tergal surface very finely and densely pilose. Pygidium regularly convex and regularly rounded at caudal edge.

Legs rather long and slender, when stretched in situ very slightly surpassing lateral edge of respective tergum. Male leg 17 (Fig. 19) with very high, somewhat irregularly shaped outer coxal lobe. Syncoxital notch of male leg 18 rather broad (Fig. 20). Male legs 19 (= telopods, Fig. 21) with a large, sublinguiform, bare to faintly setose lobe of syncoxite; lateral horns of syncoxite rather slender, setose, apically with an acuminate lappet; lateral surfaces of prefemur and femur micropapillate; caudofemoral process very prominent, angulate at base, with a distinct membranous sac distally; tarsus narrowly rounded at tip.

***Glomeris* sp.**

Material: 1 ♀ (macerated and fragmented, head missing, apparently collected dead) (DZUL), Canary Islands, La Palma, Cueva Honda de Gallegos, 7.v.2000, leg. GIET.

Remarks: Regrettably, the above specimen, the only one so far collected on La Palma island, is in too poor condition to attempt a species identification. The species in question seems to be pigmented, brownish, and is thus unlikely to be a true troglobite.

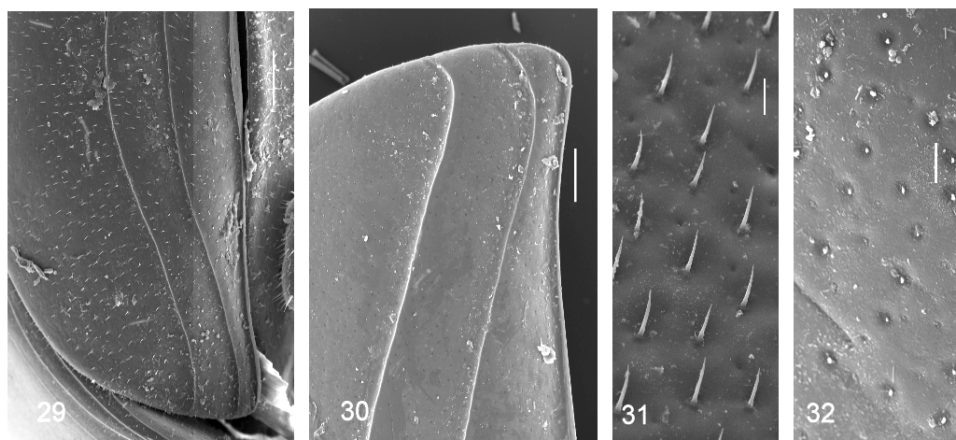
KEY TO THE CANARIAN *GLOMERIS* SPECIES

1. Body cuticle entirely pallid, distal halves of tarsi and/or lateralmost parts of terga only rarely slightly yellowish; ocelli largely depigmented, only occasionally discernible as pale brownish spotlets. Tenerife, caves. *G. speobia*
- Body at least partly pigmented (except for very early instars), colour patterns variable, ocelli always blackish brown. 2.
2. Adult body large, up to 11.5 (σ)/13.4 mm (♀) long and 6.0 (σ)/6.4 mm (♀) wide, colour pattern usually absent, entire body blackish, but sometimes very vague sublateral, strongly marbled, paler spots/markings on terga 2-10 discernible (much like in Fig. 4). Telopod caudofemoral process relatively undifferentiated, forming neither an evident angle at its base nor a considerable membranous sac at tip (Figs. 15 & 16). La Gomera. *G. canariensis*
- Adult body usually smaller, pattern of clear yellowish spots or stripes always discernible against a darker (brown to black-brown) background, sometimes pallid even dominating (especially so in smaller individuals). Telopod caudofemoral process more strongly differentiated, with a rather prominent membranous sac at tip and usually forming a slight but evident angle at its base 3.
3. Midcaudal edge of terga 3(4)-10 not sinuate; central pale spot on pygidium normally wide and trapeziform. El Hierro. *G. hierroensis*
- Midcaudal edge of terga 3(4)-10 slightly but evidently sinuate; central spot if any on pygidium only seldom trapeziform, but even then not so wide at base. 4.
4. Neither axial line nor row of pale spots on terga (Fig. 4). Gran Canaria. *G. vicentee*
- Usually an axial row of pale spots on terga 2-10. 5.
5. Body width 3.4-3.9 (σ)/3.5-5.1 mm (♀); thoracic shield normally quite widely to almost entirely pallid on sides (Fig. 3); venter and legs greyish to grey brown. La Gomera. *G. gomerana*
- Body width 2.2-3.0 (σ)/2.3-3.5 mm (♀); thoracic shield in darker specimens not so widely pallid on sides (Fig. 1), in paler individuals more like in Fig. 2; venter and legs pallid to pale brown. Tenerife. *G. alluaudi*

SYSTEMATIC-PHYLOGENETIC CONSIDERATIONS

The classification of glomeridan millipedes is a subject widely open for discussion (e.g., Mauriès, 1971; Hoffman, 1980), and until a comprehensive phylogenetic analysis has been undertaken, a conservative approach is advisable. It was in this spirit that Golovatch (1987) treated the three Canarian *Glomeris* species known at that time as an informal species-group, “the *Glomeris alluaudi*-group”. The new species described in the present paper, although considerably expanding the intra-group range of variability, do not justify a departure from this standpoint.

Nevertheless, the *Glomeris alluaudi*-group, now with six described species, appears as a well-defined, probably monophyletic group with three potential synapomorphies (cf. Table II):



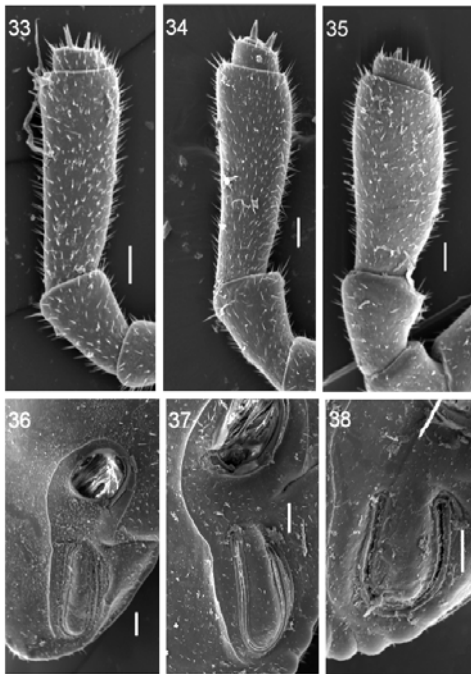
Figs. 29-32. Pilosity. – 29: *G. hierroensis*, densely pilose collum. – 30: *G. marginata* (France), naked collum. – 31: *G. canariensis*, setae from midbody tergum. – 32: *G. marginata*, vestigial setae from tergum 2. – Scanning electron micrographs. Scales 0.1 mm (29-30), 0.01 mm (31-32).

1. Tergal pilosity. All members of the *alluaudi*-group have a dense covering of setae on the terga, often most easily seen on collum (Figs. 29, 31). Non-Canarian species of *Glomeris* and related genera have naked terga, although extremely small “stumps” which may represent vestigial setae, can be seen with the scanning electron microscope (Figs. 30, 32).
2. Shape of antennomere 6. In members of the *alluaudi*-group, the largest vertical diameter of antennomere 6 is at or close to the tip (Figs. 33, 34) whereas in most continental congeners, the largest diameter occurs ca. at mid-length (Fig. 35). *G. hierroensis* comes closest to the “continental” condition. On the other hand, the S. Italian *G. albidonigra* has a quite “Canarian” antennomere 6.
3. Shape of Tömösvary’s organ. In the Canarian species, Tömösvary’s organ is particularly narrow, the length/width ratio varying from 1.8-2.8 (Figs. 36-37), compared with 1.3-1.5 in the studied continental congeners (Fig. 38). The studied species of *Hyleoglomeris* have a ratio of 1.8, just at the lower end of the *alluaudi*-group range.

Golovatch (1987) characterized the *alluaudi*-group as a well-defined species group based on four characters: tergal pilosity, long and slender antennae, very high outer lobes of male leg-pair 17, Tömösvary’s organ “almost transverse”. The first and last of these characters correspond with 1. and 3. above. The antennal character now seems insignificant, considering the newly described species and a wider study of continental congeners. The outer coxal lobe of leg-pair 17 is indeed high in Canarian species but in those where it is smallest (*alluaudi*) it is not higher than in some continental congeners (e.g., *G. albida* Mauriès & Vicente, 1977).

Table II summarizes several characters across the *G. alluaudi*-group and some related species.

We have no suggestions for the closest relative(s) of the *alluaudi*-group. Geographically, one would expect such species to occur in the Iberian peninsula and/or



Figs. 33-38. Antenna tips (antennomeres 6-7) (33-35) and organs of Tömösváry (36-38) of *G. speobia* (33, 36), *G. canariensis* (34, 37) and *G. marginata* (France) (35, 38). – Scanning electron micrographs. Scales 0.1 mm.

an independent trend within *Glomeris*. The apparent synapomorphies of the *alluaudi*-group listed above certainly support this point of view. This example of convergent evolution bodes ill for any morphology-based phylogenetic analysis of the glomerids!

CAVE GLOMERIDS

Glomeris speobia from Tenerife has been found only in caves. However, its troglomorphy is not very strongly developed: The lateral parts of the terga and the rudimentary ocelli are sometimes slightly pigmented, and the legs and antennae are not dramatically elongated compared to other species of the *alluaudi*-group. Two further Canarian *Glomeris* species have been found in the MSS (mesocavernous shallow stratum, milieu souterrain superficiel), viz. *G. canariensis* on La Gomera and *G. vicenteae* on Gran Canaria. None of these show any troglomorphic traits (the MSS specimens of *G. canariensis* are paler than most other specimens, but similarly pale specimens have also been found in entirely epigeic habitats). In mainland Europe, caves are quite often populated by members of the order Glomerida (e.g., Vandel, 1964) but the only *Glomeris* species described so far showing troglomorphic features is *G. albida* Mauriès & Vicente, 1977. *G.*

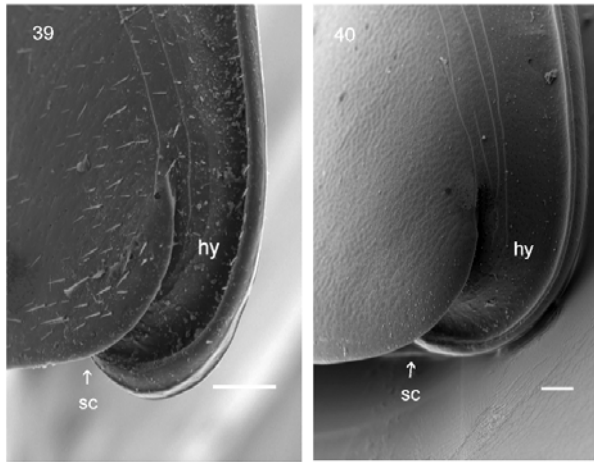
NW Africa, but we are aware of no species from these areas which approach the *alluaudi*-group in the abovelisted characters. *G. albidonigra* Strasser, 1977, is similar to the *alluaudi*-group on the antennomere 6 character, but whether this is due to synapomorphy or convergence, cannot be decided at present.

Golovatch (1987) described some morphological trends in the *alluaudi*-group bridging the gap between *Glomeris* and the closely related genus *Hyleoglomeris*. Table III summarizes his discussion, amplified with data from the newly described Canarian species. Several other characters of the *G. alluaudi*-group, however, unequivocally point to *Glomeris* rather than *Hyleoglomeris*, e.g., the four-segmented telopodites of male legs 17 (more reduced in *Hyleoglomeris*) and the relatively low number (0-4) of thoracic striae (more striae in *Hyleoglomeris*).

Golovatch (1987) argued that the trend to “hyleoglomerization” in the *alluaudi*-group should not be awarded any significance in a discussion of the relationships between these two genera but should rather be regarded as an

Table II. Selected characters in the *G. alluaudi*-group, three continental congeners and selected species of *Hylegomeris* and *Lobgomeris*. Characters providing potential synapomorphies for the *G. alluaudi*-group are shown in **boldface**.

	G. alluaudi -group										Continental species				
	<i>alluaudi</i>	<i>speobia</i>	<i>gomerana</i>	<i>canariensis</i>	<i>vicentiae</i>	<i>hierroensis</i>	<i>marginata</i>	<i>puchtra</i>	<i>albidomigra</i>	<i>H. cremea</i>	<i>H. lenkorana</i>	<i>L. pyrenaica</i>			
body pilosity	+	+	+	+	+	+	-	-	-	-	-	-			
dorsal spots	+	N.A.	+	-	+	+	-	+	-	-	+	-			
tergal sinuosity	slight	slight	slight	slight	obvious	slight	slight	-	-	slight	slight	-			
antennomere 6, rel. length (% of 3-6)	43	37	36	32	43	39	34	38	37	35	39	30			
antennomere 6 l/h	2.7	2.7	2.5	2.9	2.9	2.4	2.2	2.7	3.1	1.9	2.3	2.1			
antennomere 6 maximal width	near tip	at tip	near tip	at tip	at tip	at tip	at middle	at middle	near tip	at middle	at middle	at middle			
org. of Tömösvary l/h	1.86	2.80	1.78	2.15	2.00	2.00	1.27	1.57	1.35	1.82	1.80	1.40			
schisml/hypochsism	normal	post. (ext.) lobe reduced	normal	normal	normal	normal	normal	normal	normal	normal	normal	normal			
outer coxal lobe of ♂ leg 17	rather high, somewhat variable	very high, somewhat irregularly shaped	high, somewhat variable	high, somewhat variable	N.A.	very high, somewhat irregularly shaped	lower			higher					
caudomesal femoral process of the telopods, angulation	yes	no	no	no	yes	yes	no			yes					
caudomesal femoral process of the telopods, membranous sac	distinct	distinct	distinct	absent or poorly developed	distinct	distinct	no			yes					



Figs. 39-40. Right lateral lobes of thoracic shield (tergum 2), showing the reduced hyposchism in *G. speobia* (39) compared with the normal condition in *G. canariensis*. – Scanning electron micrographs. Scales 0.1 mm. – hy: hyposchism, sc: schism.

albida (known from a cave in prov. Malaga, southern Spain) is entirely depigmented (including ocelli). *G. speobia* thus becomes the second *Glomeris* species showing signs of troglomorphism. Still, no member of the genus is as pronouncedly troglomorphic (loss of ocelli, elongation of legs and antennae, depigmentation of body teguments, sometimes also “cave gigantism” and cuticle weakening) as certain species in the related genera *Typhloglomeris* Verhoeff, 1898, *Trachysphaera* Heller, 1858, *Doderia* Silvestri, 1904, *Speleoglomeris* Silvestri, 1908, *Hyleoglomeris* Verhoeff, 1910

and a few others.

The situation with cave-dwelling in *Glomeris* strongly reminds of the Central and East Mediterranean genus *Typhloglomeris*, where most of the species are purely epigean (all referred to the apparently superfluous genus *Albanoglomeris* Attems, 1926), two are geobionts, and another two are strict trogllobionts (cf. Golovatch, 1989). All the geo- and trogllobionts in *Typhloglomeris* are virtually entirely pallid. Similarly, the only hitherto documented geo- to troglophilic *Hyleoglomeris*, the Caucasian *H. lohmanderi* Golovatch, 1975, is also entirely depigmented.

BIOGEOGRAPHY AND ECOLOGY

In the absence of any substantiated phylogenetic hypothesis, the *G. alluaudi*-group at present delivers no information about external biogeographical relationships of the Canary Islands. However, being apparently a monophyletic group, it constitutes one of the endemic “species swarms” so characteristic of the Canary Islands. With only six described species (plus possible one undescribed from La Palma) it is only a small swarm. However, like the vast majority of species in the better known swarms, each species of the *G. alluaudi*-group is confined to one island (Enghoff & Báez, 1993). The absence of *Glomeris* species from Lanzarote and Fuerteventura is not surprising: these islands are too dry to support such generally hygro- to mesophilic forms as glomerids.

Pill-millipedes are unknown from the other Macaronesian archipelagos (Azores, Madeira, Cape Verdes) (Enghoff, 1992a) which, in part, are host to several other species swarms of millipedes. The julid genus *Dolichoilus* (Enghoff, 1992b) is by far the largest, with 46 species on the Canary Islands and a handful of further species on Madeira, the Salvages (tiny islets between Madeira and the Canary Islands) and the Cape Verdes, and

Table III. Morphological trends in the *G. alluaudi*-group, compared with typical conditions in *Glomeris* and *Hyleoglomeris*, based on Golovatch (1987).

	typical <i>Glomeris</i>	<i>canariensis</i>	<i>speobia</i>	<i>gomerana</i>	<i>vicentiae</i>	<i>alluaudi</i>	<i>hierroensis</i>	<i>Hyleoglomeris</i>
body size	generally larger	largest in group	relatively large	medium	relatively large	relatively small	smallest in group	generally smaller
caudo-femoral telopod process	not angulate	not angulate	not angulate	not angulate	slightly but distinctly angulate	slightly but distinctly angulate	clearly angulate	clearly angulate
caudo-femoral telopod process membranous sac	absent	absent or small	well-developed	well-developed	well-developed	well-developed	well-developed	well-developed

3-4 continental species (one of these has been introduced to the Canary Islands, Enghoff 2002). The *Cylindroiulus madeirae*-group (Enghoff, 1982; Read, 1989) has 30 species on Madeira, one of which is shared with the Azores, and an endemic species in the Canary Islands. Finally, the blaniulid genus *Acipes* (Enghoff, 1983) has 6 species on Madeira, one in the Canary Islands and two in continental Spain (Enghoff, 1986; Enghoff & Mauriès, 1999).

Species of the *G. alluaudi*-group other than the troglobiont *G. speobia* have frequently been collected in rotten wood, but also in leaf litter. In La Gomera, the only island hosting two epigeal species, both at least partly occur syntopically. This is remarkable as even in the most species-rich parts of mainland Europe only a few places in, e.g., northern Italy and Croatia support two or three narrowly co-existing *Glomeris* species. A single *Glomeris* species per site/habitat is the general rule.

The two Gomeran species seem to have slightly different habitat requirements. During HE's fieldwork in 1989, both species were found strictly syntopically in two cases. In one case, *G. gomerana* was found sitting on the underside of a stone, while *G. canariensis* was found in litter under the same stone. In another case, *G. gomerana* was found superficially in a log, while *G. canariensis* was found deeply inside the same log. It would thus seem that the more aposematically coloured *G. gomerana* tends to occupy more exposed microhabitats than the almost unicoloured, dull *G. canariensis*. The recent finds of *G. canariensis* in the MSS support this idea.

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ADDENDUM

Recently, several *Glomeris* cf. *speobia* (2♂, 4♀, DZUL) were collected on TENERIFE, Monte del Agua, El Picón, MSS, 21.i.2003, leg. H. Contreras. The specimens are depigmented like *G. speobia*, but they are smaller (body width of males 2.4-2.5 mm). Whether or not they are conspecific with the type material of *G. speobia* must await a comprehensive comparative analysis.