

The *alluaudi*-group of *Glomeris*, another Macaronesian species swarm in millipedes (Diplopoda: Glomeridae)

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Glomeris alluaudi Brölemann, 1900 (type-species of *Trichoglomeris* Verhoeff, 1906) and *G. gomerana* Attems, 1911, both redescribed upon newly collected topotypes, as well as *G. canariensis* sp.n., all endemic in the Canary Islands, are shown to form a distinct species-group within *Glomeris* Latreille, 1802–03 (*Trichoglomeris* being another of its numerous junior synonyms). Like several other millipede genera, the *alluaudi*-group seems to form a species swarm in Macaronesia.

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The first glomerid millipede described from Macaronesia was *Glomeris alluaudi* Brolemann, 1900 from Tenerife, Canary Islands. Despite the fact that Brolemann (1900) had erected his taxon for a single female, Verhoeff (1906) regarded the peculiar tergal pilosity in *G. alluaudi* sufficient for creating an independent genus, *Trichoglomeris*. Soon after that Attems (1911) described a second Canarian *Trichoglomeris*, *G. gomerana*, from Gomera, though cautiously referred to Verhoeff's category as a subgenus of *Glomeris*. Indeed, Attems (1911) had good reasons to do so, because he had at hand a series comprising males. He noticed that the telopod structure of his *G. gomerana*, the crucial character for generic allocation in the Glomerida, was practically identical to that of the numerous European *Glomeris* species.

However, later on both Attems (1926) and Verhoeff (1926–32) resurrected *Trichoglomeris* to full generic status, though the latter author still retained it for the type-species only. In his latest reclassification of the Diplopoda, Hoffman (1979) practically agreed with Verhoeff's decision, although Mauriès (1971) had expressed serious doubts as regards the generic rank of *Trichoglomeris* and had even discarded this name from his own system of the Glomerida¹.

In short, the finding of male topotypes of *Glomeris alluaudi* was crucial for solving the whole riddle, while the existence of *G. gomerana*, externally a good *Trichoglomeris*, but anatomically an indisputable *Glomeris*, was only an indirect and often ignored indication.

Material and acknowledgements. Through the kind assistance of Dr. H. Enghoff, Universitetets Zoologiske Museum, Copenhagen (ZMUC), Dr. J. Gruber, Naturhistorisches Museum Wien (NHMW), Dr. J.-P. Mauriès, Muséum National d'Histoire Naturelle, Paris (MNHP), and Dr. K. Thaler, Institut für Zoologie der Universität Innsbruck, I have been privileged not only to restudy the type specimens of both *G. alluaudi* and *G. gomerana*, but also to examine new, topotypical material. The fresh sample from Tenerife, made by Dr. K. Thaler, has turned out to contain a male of *G. alluaudi*, this making it possible to judge on the true status of *Trichoglomeris*. No less interesting, two samples from Gomera, both belonging to the Copenhagen Museum, comprised, besides *G. gomerana*, a new species.

Before going further, I should like to extend my sincere thanks to the abovementioned persons.

¹ Perhaps on geographical rather than morphological considerations, Mauriès (1971) regarded *Trichoglomeris* (non *Trichomeris* – this must be a typographical error) a nomen dubium sub *Loboglomeris*, a genus restricted to the Pyrenees and Canabrie Mountains.

TAXONOMY

Glomeris alluaudi Brolemann, 1900

Figs. 1, 2, 4-6.

Glomeris Alluaudi Brölemann, 1900: 439; type-locality: Tenerife, forest "Las Mercedes" near La Laguna.*Material studied*: Holotype ♀ (MNHP), Tenerife, forest "Las Mercedes". 750 m, 30.V.1890. Alluaud. - 1 ♂, 2 ♀ (NHMW, Thaler ded.), Tenerife, Orotava, Aguamansa, 1100-1400 m. 13, 16 & 17.11.1982, Thaler.*Diagnosis*. Differs from other Canarian species by the particularly small body size (width less than 3.0 mm), relatively low outer coxal lobes of leg-pair 17 in ♂, narrowly ogive syncoxite notch of leg-pair 18 in ♂, smaller suboval median lingual lamina of the telopods, etc.*Notes*

The original description of *G. alluaudi* is rather accurate (see Brolemann 1900), though incomplete. The holotype is now considerably faded, yet the colour pattern is still identifiable (cp. Figs. 1 & 2). In the fresh topotypes, the colour is bright (especially in ♂), background dark brown, spots or markings whitish-yellow, ventrum and legs pale yellowish-brown. Body particularly small (up to 4.9 mm long in topotypes, 2.5 mm wide in holotype, 2.2 and 2.9 mm wide in ♀ topotypes, 2.9 mm wide in ♂ topotype). Ocelli 6 + 1 (holotype) or 7 + 1 (topotypes). Antennae slender and long, antennomere 6 2.5-2.6 times as long as wide. Head beset with rather long and dense setae below level of antennal sockets. Coxium with two usual transverse striae. Thoracic shield with three (holotype and topotypes) or four (topotype ♀) striae, of which only the last one starts a bit dorsad of the schism and the two or three posteriormost ones cross the dorsum; hyposchism reaching to hind tergal contour, but not exceeding it. Terga 5-11 with a very slight median sinuosity of hind margin. Entire tergal surface finely pilose.

♂: Pygidium without modifications, roundly convex like in ♀. Leg-pair 17 (Fig. 4) with relatively high outer coxal lobes, telopodite 4-jointed, somewhat reduced. Leg-pair 18 (Fig. 5) with a narrowly ogive syncoxite notch, telopodite 4-jointed. Telopods (Fig. 6) particularly incrassate; syncoxite lateral horns rather thick, high and setose, each crowned with a setoid, median lingual lamina subcircular, not particularly wide; large

caudo-femoral process with a well-developed distal membranous sac, basally more *Hyleoglomeris*-like.

Glomeris gomerana Attems, 1911

Figs. 3, 7-9.

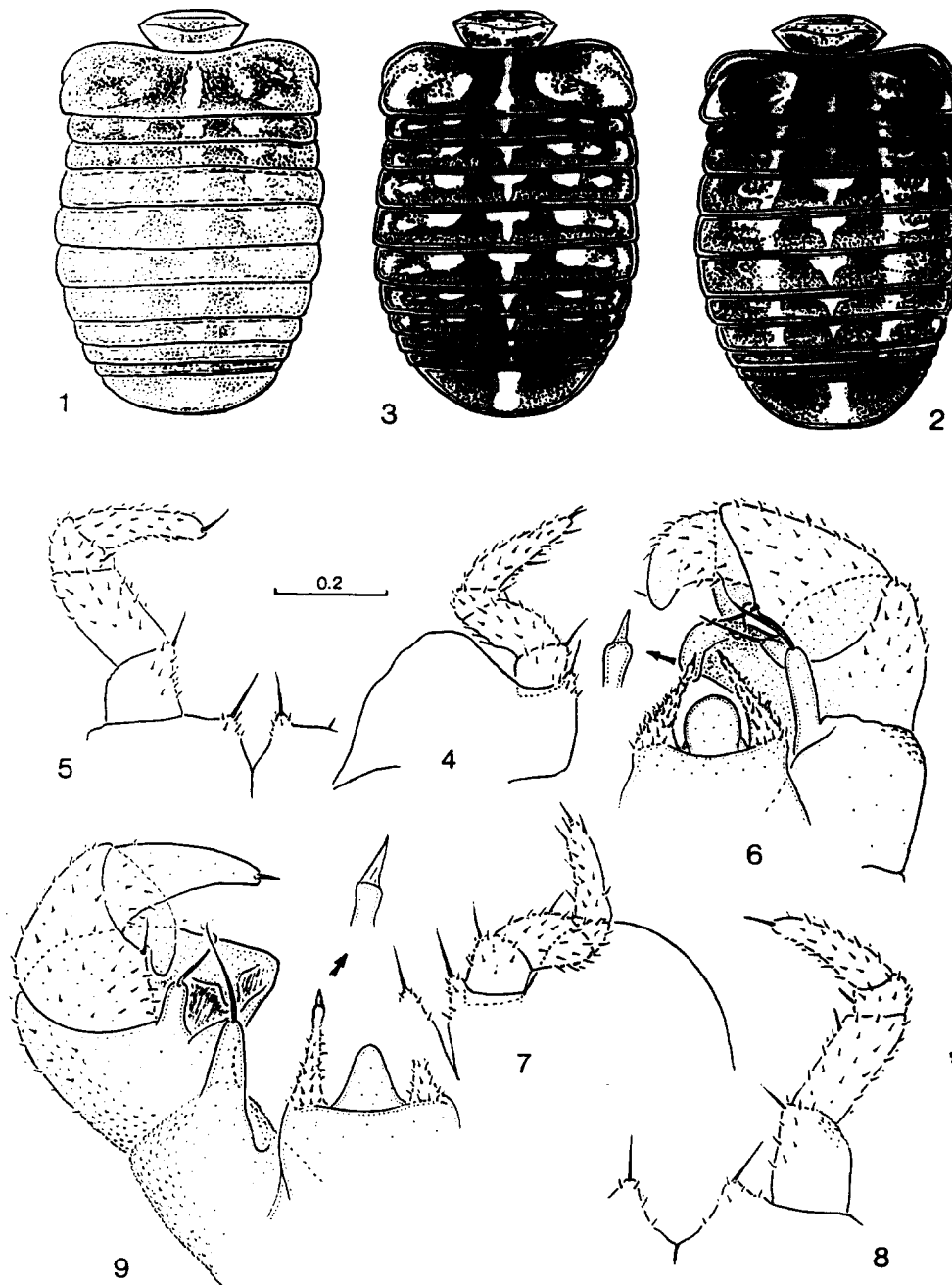
Glomeris (Trichoglomeris) gomerana Attems, 1911: 111; type-locality: Gomera, Cumbre del Carbonero.*Material studied*: 1 ♂, herewith designated as lectotype³, Gomera, Cumbre del Carbonero, 14.I.1908, May (NHMW). - Paralectotypes: 1 ♂ (dissected), 1 ♀ (intact), 1 head, 2 slides, same data as lectotype (NHMW)⁴. - 1 ♂, 1 ♀ (ZMUC), Gomera, pine forest, 1200 m. XI.1978, J. Rabøl.*Diagnosis*. Differs from Canarian congeners by the medium-sized body (width 3.4-4.1 mm), higher outer coxal lobes of leg-pair 17 in ♂, roundly triangular median lingual lamina of the telopod syncoxite, papillate telopod femur, etc.*Notes*

Attems (1911) must have been misled by Brölemann's (1900) description of the colour pattern in *G. alluaudi* to state that his *G. gomerana* was quite distinct by this character. On the contrary, a (re)study of pertinent material shows that by coloration *G. gomerana* is barely distinguishable from *G. alluaudi* (cp. Figs. 2 & 3). However, in *G. gomerana* the thoracic shield is generally much more broadly pale along lateral and antero-lateral margins, ventrum and legs are brown, background colour of terga is blackish-brown, spots and markings dull yellowish. This pattern concerns the fresh specimens only, while the types are all much faded, though, e.g., the wide pale patches on the thoracic shield are still traceable. Body medium-sized, 3.4-4.1 mm wide, up to 5.6 mm long. Ocelli 7 + 1 (lectotype) or 8 + 1 (both paralecto- and topotypes). Antennae long and slender, antennomere 6 c. 3.2-3.3 times longer than wide. Collum

³ Even the faded ocelli in the holotype distinctly show the number of 6 + 1 (perhaps even 7 + 1, because the anteriormost couple of ocelli is known to be particularly small and sometimes barely visible), not 5 + 1 as stated in the original description by Brölemann (1900).

⁴ As there are two slides with mounted telopods and only one dissected male in the tube, it seems impossible to attribute with certainty this male to either slide. Therefore I have designated the only intact male as lectotype.

⁵ According to Weidner (1960), four additional syntypes are kept in the Zoologisches Institut u. Zoologisches Museum der Universität Hamburg.



Figs. 1-9. *Glomeris* spp. — 1-3. Habitus, dorsal; (1) *G. alluaudi* Brolemann, holotype 9.2.5 mm wide; (2) same, topotypic ♀, 2.9 mm wide; (3) *G. gomerana* Atterns, topotypic ♀, 4.0 mm wide. — 4-6. *G. alluaudi*, topotypic ♂; (4) leg-pair 17; (5) leg-pair 18; (6) telopods. — 7-9. *G. gomerana*, topotypic ♂; (7) leg-pair 17; (8) leg-pair 18; (9) telopods. — Scale (4-9): 0.2mm.

with two usual transverse striae. Thoracic shield with three or four striae, of which the posterior one starts a bit above the schism and the one or two middle ones cross the dorsum; hyposchism reaching to hind tergal contour, though not projecting beyond it. Terga 5–11 with a very slight medial sinuosity of hind margin. Surface of terga finely pilose.

♂: Pygidium without modifications, roundly convex like in ♀. Leg-pair 17 (Fig. 7) with higher outer coxal lobes. Leg-pair 18 (Fig. 8) with a wide ogive syncoxite notch. Telopods (Fig. 9) with a high and more or less roundly triangular lingual lamina of syncoxite, caudo-femoral process massive, typically *Glomeris*-like, but with a distal membranous sac.

Glomeris canariensis sp. n.

Figs. 10–12.

Material studied: 1 ♂ (holotype), 1 ♀ (paratype) (ZMUC) Gomera, launsilva, under stones and leaves, X-XI.1978 J. Rabøl.

Diagnosis. Differs from Canarian congeners by larger body size (width 5.2–6.0 mm), uniform blackish coloration devoid of spots or markings, higher outer coxal lobes of leg-pair 17 in ♂, larger syncoxite median lingual lamina of the telopods, etc.

Description

♂: Length c. 10 mm, width 5.2 mm. Colour blackish-brown, without any spots or markings even on collum; only lateral and hind tergal margins pale whitish; ventrum, legs and labium pale brownish. 9 + 1 black convex ocelli on each side. Head setose below level of antennal sockets. Antennae long and slender, with usual four apical cones; antennomere 6 c. 3.2 times as long as wide. Tömösvary's organs almost transverse, as in both *G. alluaudi* and *G. gomerana*. Collum with two usual transverse striae. Thoracic shield with three striae, all beginning beneath schism, only the 2nd cross the dorsum; hyposchism rounded regularly, reaching to hind tergal contour, but not projecting caudad beyond it. Terga 5–10 medially very slightly sinuate at hind margin. Tergal surface very finely and densely pilose. Pygidium regularly rounded, without modifications.

Leg-pair 17 (Fig. 10) with particularly high outer coxal lobes, telopodite somewhat reduced, 4-jointed. Leg-pair 18 (Fig. 11) with a broadly

ogive syncoxite notch, telopodite 4-jointed. Telopods (Fig. 12) with a particularly large, rounded, finely setose lingual lamina of syncoxite, lateral horns thick, setose, apically pointed, subapically with a tiny lobule (alike *G. gomerana*); caudo-femoral process huge, without membranous sac, almost concealing fronto-femoral flagelliferous finger; tarsus not pointed, rounded.

♀: Length c. 10.2 mm, width 6.0 mm. Other non-sexual characters as in ♂.

The *alluaudi*-group

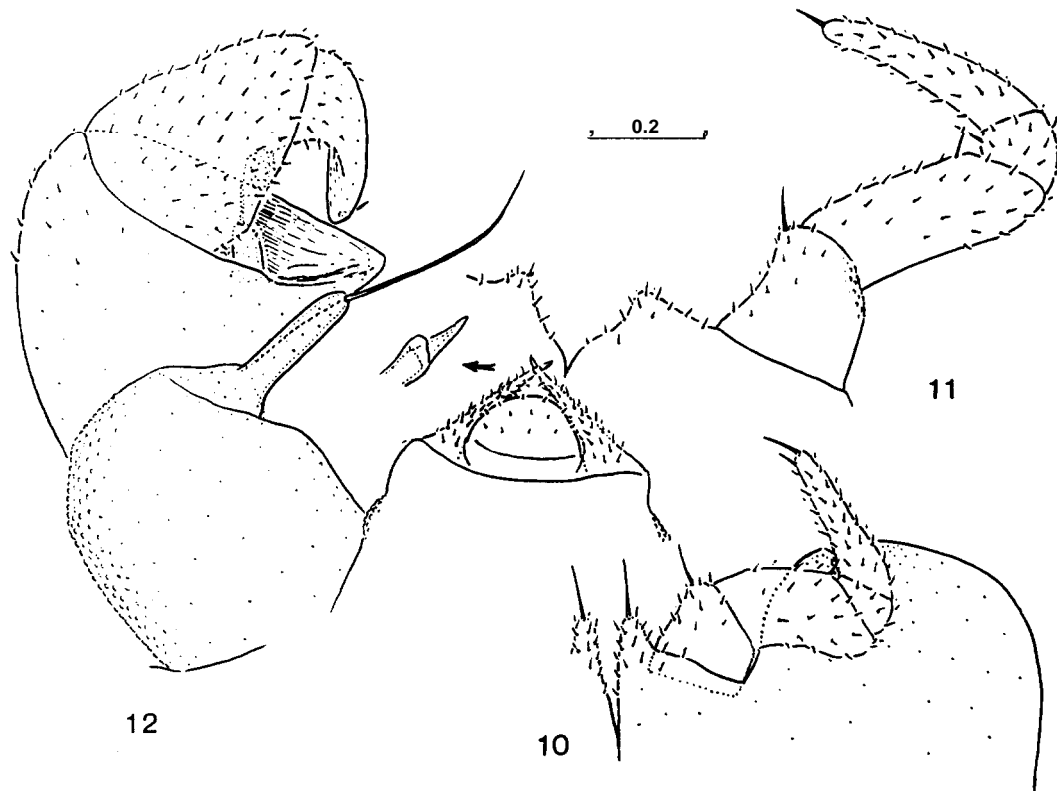
The Canarian *Glomeris alluaudi*, *G. gomerana*, and *G. canariensis* certainly form a well-defined species-group within this large Euro-Mediterranean genus. This group may be called the *alluaudi*-group, with the following characters: (1) micropilosity of the terga; (2) unusually long and slender antennae (like in some cavemicoles); (3) outer coxal lobes of leg-pair 17 in ♂ unusually high (rather reminding of *Hyleoglomeris*); (4) Tömösvary's organs almost transverse.

However, this set of characters seems hardly sufficient to warrant a separate (sub)generic rank, because the groundplan telopod structure is indisputably *Glomeris*-like. Thus the name *Trichoglomeris* Verhoeff, 1906 must join the long list of junior synonyms of *Glomeris* Latreille, 1802–03 (see Hoffman 1979).

What seems particularly interesting is the fact that within the *alluaudi*-group we find a parallel to the general trend of complication of the primitive *Glomeris*-like telopod type into that met with in the more advanced genus *Hyleoglomeris*. The latter is known to comprise a rich variety of usually medium- to smaller-sized species in the Oriental realm, the Himalayas, Middle Asia, the Caucasus, Asia Minor and even the Balkans. Such forms possess usually an increased number of striae on the thoracic shield, a more pronounced reduction of leg-pair 17 in ♂, and a strongly differentiated caudo-femoral process of the telopods.

In *G. alluaudi*, this process is practically *Hyleoglomeris*-like, in both *G. alluaudi* and *G. gomerana* it is provided with a well-developed distal membranous sac (as in *Hyleoglomeris*), and in all the three Canarian species leg-pair 17 in ♂ is reduced in a more *Hyleoglomeris*- than *Glomeris*-like way.

Biogeographically, two reasonable alternatives



Figs. 10–12. *Glomeris canariensis* sp.n., ♂ holotype; (10) leg-pair 17; (11) leg-pair 18; (12) telopods. — Scale: 0.2 mm.

can be proposed to explain the distribution of *Glomeris* and *Hyleoglomeris*, both implying an ancient age of the Macaronesian swarm. One alternative seems particularly consistent with the traditional view of the origin of the Mediterranean nemoral biota from the Oriental one (see Heptner 1936; Wulff 1944; etc.), and thus is postulating the predominance of ancient migrations westwards. Such a view has quite a solid paleontological background as well; the hardwood genera *Quercus*, *Fagus*, *Pyrus* and others are good examples of Oriental elements migrating along the northern coast of the declining Tethys Sea in Early-Middle Tertiary (see Menitsky 1982; Zhilin 1984; etc.).

Taking into account the recent discoveries of two *Hyleoglomeris* species in the Balkans (see Mauries 1984) linking the modern ranges of *Glomeris* and the more advanced *Hyleoglomeris*, it

seems reasonable to surmise that an early *Glomeris*-like type first become established throughout Eurasia and later split into *Hyleoglomeris* in the east and present-day *Glomeris* in the west. If so, *Hyleoglomeris* may be seen as a relatively young (monophyletic?) taxon which, besides *Rhopalomeris*, is the only genus of the advanced glomerid tribe Trachysphaerini *sensu* Mauries (1971, 1984) that populates the Oriental Region (along with the Mediterranean, this is the major centre of generic radiation in the entire order Glomerida), and is the only glomerid genus occurring between Indochina and the Aegean Sea (the largest known generic range in Glomerida). In other words, the old idea of its Oriental origin and expansion to the west (probably in Late Paleogene-Early Neogene) may be regarded as plausible (see Golovatch 1975).

On the other hand, though the following suppo-

sition is less consistent with biogeographical and paleontological evidence, it seems not too improbable that an early Glomeris-type, perhaps during Early Tertiary in Europe, could have given rise to Hyleoglomeris and allied genera (see Mauriès 1984). An eastward dispersal could then have followed the northern coast of the regressing Tethys Sea. Several western relicts, including both the Balkan species, obviously of the most ancient stock, may have survived only as cavernicoles.

However, in the context of the origin of the alluaudi-group of Glomeris, it matters little whether Hyleoglomeris, nowadays almost exclusively Asian, originated in situ or is migrant from the west. What seems important is the fact that the "hyleoglomerization" within the Macaronesian species swarm must have taken place independently and long ago, perhaps in Miocene-Early Pliocene, and from a true Glomeris-type. At least among the 13 currently known Glomeris species and subspecies of continental Spain (see Vicente 1981), there is no parallel to the development in the alluaudi-group.

It is no news that the Macaronesian millipede fauna is rich (about a hundred species and subspecies), comprising not only a lot of endemic forms, but also a number of (sub)endemic species-groups and (sub)genera. Such are the huge madeirae-group of *Cylindroiulus* chiefly restricted to Madeira (Enghoff 1982b, 1983b), the genus *Acipes* containing six species from Madeira and one each from the Canary Islands and mainland Spain (Enghoff 1983a, 1986), as well as *Dolicho-iulus* encompassing a good number of species from Sicily, France, Northwest Africa, mainland Spain and about a dozen species from the Canaries, two from Madeira and one from the Cape Verde Islands (cf. Mauriès 1970, 1982; Enghoff 1982a, b). And now the alluaudi-group of Glomeris must join such examples of Macaronesian species swarms.

Interestingly, within the Canarian *alluaudi*-group, body size diversity is great like in the other known instances of insular species swarms in millipedes (see Enghoff 1983b). Most probably this is also due to niche segregation. But another interesting point is the question whether the "hyleoglomerization" within the alluaudi-group went along with a decrease in body size. The larger *G. canariensis* (and its habitat?) might then be regarded as the most ancestral species of the *alluaudi*-group.

Key to the species of the *alluaudi*-group of *Glomeris*

1. Terga with a distinct colour pattern (Figs. 2.3); body much less than 5 mm wide; outer coxal lobes of leg-pair 17 in ♂ not high (Figs. 4, 7); telopod femur with a large caudal process provided with a membranous sac, syncoxite median lingual lamina not broad, at most semi-circular (Figs. 6, 9) 2
- Terga without distinct colour pattern, uniformly blackish-brown; body more than 5 mm wide (in adults); outer coxal lobes of leg-pair 17 in ♂ extremely high (Fig. 10); telopod caudal femoral process devoid of membranous sac, syncoxite median lamina very broad and regularly rounded (Fig. 12) *canariensis*
2. Body less than 3 mm wide; antennomere 6 c. 2.5 times longer than wide; outer coxal lobes of leg-pair 17 in ♂ low (Fig. 4); telopod median lingual lamina of syncoxite semi-circular, femur not papillate, caudo-femoral process well differentiated (Fig. 6) *alluaudi*
- Body width 3.4–4.1 mm; antennomere 6 more than 3 times as long as wide; outer coxal lobes of leg-pair 17 in ♂ high (Fig. 7); telopod median lingual lamina of syncoxite roundly triangular, femur at least proximally papillate, caudo-femoral process poorly differentiated (Fig. 9) ...
..... *gomerana*

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