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STUDIES ON THE MORPHOLOGY AND SYSTEMATICS OF THE TENERIFFIIDAE (ACARI, PROSTIGMATA).

1: A NEW SPECIES OF NEOTENERIFFIOLA FROM NAMIBIA

BY Mark JUDSON

ABSTRACT: Neoteneriffiola Hirst is removed from synonymy with the poorly known genus Parateneriffia Thor. A new species, Neoteneriffiola coineaui, is described from Namibia. This species can be readily distinguished from N. luxoriensis Hirst (rev. comb.), by its large size; strong, linear neotrichy of the pedal solenidia; and the relatively large dorsal plates of the opisthosoma.

A detailed study of the morphology of N. coineaui is presented. The following characters are recorded for the first time in Teneriffiidae: two pairs of prodorsal trichobothria; a distinct, pigmented ventro-median eye on the naso; two pairs of stigmata and tracheae with common atria; and sexual dimorphism of the pedal solenidia. The homologies and notations of the podocephalic and infracapitular glands of Prostigmata are discussed. A gland duct homologous with gl. c III of Caeculidae and the 'Lassenia-organ' of certain Parasitengona, is demonstrated in Teneriffiidae. The oncophyse of the chelicera bears a hollow, spine-like process which may represent the duct of a cheliceral gland. The process of the palpal tibia is here named the palpal oncophyse.

Heteroteneriffia mortoni Luxton is transferred to the genus Teneriffia Thor (n. comb.).


Une étude morphologique détaillée de N. coineaui est présentée. Les caractères suivants sont signalés pour la première fois chez les Teneriffiidae: deux paires de trichobothries prodorsales; un oeil net médian, impair et bien pigmenté sur la surface ventrale du naso; deux paires de trachées avec atria communs; et un dimorphisme sexuel des solénidies des pattes. Les homologies et les notations des glandes podocephaliques et de leurs ducts chez les Prostigmates sont discutées. Le ductus d’une glande homologue de celle de gl. c III des Caeculidae et le ‘Lassenia-organ’ de certains Parasitengona est mis en évidence chez les Teneriffiidae. L’oncophyse de la chélicère porte un process spiniforme, creux, qui représente peut-être le ductus d’une glande. Le processus du tibia du palpe est nommé l’oncophyse du palpe.

Heteroteneriffia mortoni Luxton est transféré dans le genre Teneriffia Thor (n. comb.).

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INTRODUCTION

The Teneriffiidae Thor is a poorly-known prostigmatic family, currently represented by eleven species from North America, Europe, North Africa, Central Asia, South America, Australia and the Far East. Relatively little information is available about their basic morphology and even less is known about their biology. In this paper a detailed description of a new species of Neoteneriffiola, collected in Namibia, is presented. It is hoped that this will provide a basis for future research on Teneriffiidae and facilitate comparisons with other Prostigmata.

The genus Neoteneriffiola was created by Hirst (1924) for the Egyptian species N. luxoriensis Hirst. Subsequent authors (Ehara, 1965; Tibbetts, 1958; Wainstein, 1969) added new species from Japan, U.S.A. and Tajikistan. McDaniel et al. (1976) synonymized Neoteneriffiola with Parateneriffia Thor, transferring N. luxoriensis and N. uta Tibbetts to the latter genus (N. japonica Ehara and N. tadjikstanica Wainstein were overlooked). Neoteneriffiola coineaui n.sp. is the first teneriffiid to be described from the Ethiopian region; the Neoteneriffiola species recorded from “Southern Africa” [Natal; P.D. Theron, in litt.] by Meyer (1973) remains undescribed.

METHODS

Teneriffiids are rather fragile, soft-bodied mites, which are usually crumpled by fixation in alcohol. In order to return them to something like their normal state, they can be placed in 50% lactic acid in a partially-covered cavity slide and left for a day or two at room temperature. They can then be gently warmed until the body expands. The pigmentation of the eyes should be observed before heating, as this soon disappears. Particular care has to be taken with gravid females, which readily burst due to over-expansion of the body contents — the slow clearing methods described by Coineau (1974) and Judson (1992) may help in such cases. Because of difficulties involved in obtaining completely cleared material, it is sometimes useful to first macerate specimens in cold, dilute KOH for several hours to study internal cuticular parts (e.g. the podocephalic gland ducts). Prolonged preservation of teneriffiids in lactic acid is not recommended: there is the danger that the specimens will rupture, and the setae lose their colour and become difficult to observe in detail.

The terms used here generally follow Coineau (1974) and Hammén (1980); the notations of the prodorsal setae are those proposed by Grandjean (1943a) for Anystis (Anystidae), as the homologies between the two seem certain. All the specimens figured are from the type locality. As no stases before the deutonymph are available, information given on development here is inevitably preliminary. It should be kept in mind that the ontogenetic designations given on the figures (n3, A) only refer to the post-deutonymphal stases — the absence of such a notation does not imply that the organ is larval. All measurements are given in micrometers (μm).

Genus Neoteneriffiola Hirst, revised status

Neoteneriffiola, Hirst, 1924: 1078 (type species Neoteneriffiola luxoriensis Hirst, 1924, by monotypy).


McDaniel et al. (1976) synonymized Neoteneriffiola, Austroteneriffia Womersley and Mesoteneriffia Irk with Parateneriffia Thor, without having seen material of the type species of any of these genera. Unfortunately, the types of Parateneriffia bipeclinata Thor appear to have been lost: they are not in the Museum für Naturkunde, Berlin (M. Moritz, in litt.) and Thor’s personal collection was destroyed after his death (Zacharda, 1980). As the original description of this genus is inadequate by modern standards, its identity will remain uncertain until a suitable neotype can be designated for P. bipeclinata. The synonymies proposed by McDaniel et al. seem premature and I prefer to retain Neoteneriffiola as a valid genus, pending clarification of Parateneriffia.

The situation is further complicated with respect to the new species described below, as it apparently
stands well apart from *N. luxoriensis*. It can be separated from *luxoriensis* (and all other Teneriffiidae) by the strong, linear neotrichy of the pedal solenidia; the relatively large dorsal plates of the opisthosoma; the reduced form of the peritremes; and details of the pedal chaetotaxy. Once other species of *Neoteneriffiola* become better known, it may be that these differences will warrant the erection of a new genus for *N. coineaui*.

**Neoteneriffiola coineaui** new species (figs 1-8)

**Material examined**


**Etymology**

This species is named after Prof. Y. COINEAU, in recognition of his contributions to acarology.

**Description**

**General appearance.** — Large species, idiosomal length ♀ 1030-1080, ♂ 1020-1150, tritonymph 740-1040, deutonymph 620-680. The idiosoma becomes relatively broader in successive stases, mainly due to the increasing size of the opisthosoma; opisthosoma of female relatively longer and broader than that of male. Colour of preserved specimens light tan. Soft cuticle covered by fine, unbroken, epicuticular striae; striation becoming even finer when it passes over sclerotized parts. The number of striae increases during growth, making them relatively less apparent in later stages. Setae of dorsal surfaces long, brown and barbed; base filled by actinoplin, but actinoplin is weak or absent in rest of seta, leaving a hollow lumen (e.g. fig. 6C).

**Prodorsum** (fig. 1A). — With a thin, but distinct, sclerite, distinguished from the surrounding cuticle by its much finer striation and by the presence of pores. This sclerite is composite: setae *c*₁ have moved anteriorly and their microsclerites have fused with the prodorsal sclerite. The sclerite therefore bears three pairs of ordinary setae (*na*, *np* and *c₁*) and two pairs of trichobthria (*sa*, *sp*). Trichobthria finely barbed; *sa* directed anteriorly, *sp* dorsolaterally. Bothridium of *sa* small and typical in form; *sp* with 12-15 tubular vesicles (forming the "rosette") opening just below the internal rim of the bothridium (fig. 1D); cuticle around *sp* raised into irregular folds. Seta *na* situated on a slight tubercule, with *sp* at the base. Sclerite with two rows of tendons (*pt*), without an internal ridge, representing the bases of cheliceral retractor muscles. Naso (fig. 1F) broad, not clearly delineated from anterior margin of prosoma in dorsal view; bearing a distinct, undivided lens on its ventral surface, but without any differentiation of the thick dorsal cuticle above. Above the lens lies a weak, but distinct, ring of pigment granules (*pm*). Lateral eyes large, separate, without a sclerite, posterior pair slightly smaller than anterior pair. Anterior eyes with a distinct cornea of clear cuticle extending to the pigment below. Pigment of anterior eyes dark, forming a cup-shape around the corneas. Pigment of the posterior pair lighter, appearing white in reflected light, with a less well defined form. No trace of an intercheliceral gland was found.

**Opisthosoma.** — With only 6 segments; paraproctal segment PS. Four pairs of lyrifissures (cupules *ia*, *im*, *ip*, *ih*) present. Chaetotaxy holotrichous; dorsal setae long, decreasing in length caudally; setae *c₁* and *c₂* subequal in length. Setae dark and bearing five rows of low, wedge-shaped barbs; actinoplinous core limited to base of setae. Paraproctal lips each with three, short, barbed setae. Five pairs of sparsely barbed aggenital setae present, without microsclerites. Progenital lips with a thin strip of sclerotized cuticle (reduced in male, fig. 4E); 2 pairs of genital setae appearing in tritonymph, increasing to 5-8 pairs in male and 6-8 pairs in female. An incomplete fold is present ventrally, interpreted as representing the anterior margin of the opisthosoma.
FIG. 1: *Neoteneriophiila coineau* n. sp., female (unless otherwise indicated).

A. — Dorsal view, chelicerae extended; legs and right palp removed; striae only shown in part (about every fifth stria drawn); arthrodial membranes of epimera shown on left side only. B. — Distal segments of right palp, paraxial view (tarsus stippled for clarity). C. — Right lateral eyes, dorsal view. D. — Detail of palpal oncophysis, ventrolateral view. E. — Right bothridium sp, dorsal view. F. — (Male) anterior part of prodorsum, lateral view, showing naso and median eye; chelicerae and peritremes omitted.

Abbreviations: *b.PD* border of prodorsum; *b.sc.* border of prodorsal sclerite; *OCm* median eye; *op* oncophysis; *ops* sclerite of oncophysis; *pm* pigment of median eye; *pt* prodorsal tendons; *TG* tegulum; *ves* bothridial vesicle.
FIG. 2: Neoteneriffiola coineaui n. sp., female.

A. — Ventral view; chelicerae extended; legs and palps removed; striae only shown in part (about every fifth stria drawn). B-D. — Distal end of right chelicera in (B) paraxial, (C) distal and (D) dorsal views.

Abbreviations: ap epimeral apodeme; ap.sj sejugal apodeme; as sternal apodeme; bas base of apotele; cs cheliceral stylet; k condyle; mag aggenital muscles; mi lower jaw (apotele) of chelicera; op oncophysis; ti inferior tendon, ts superior tendon of chelicera; ϕ pharynx.
FIG. 3: Neoteneriffiola coineaui n. sp., female.

A. — Dorsal view of prosoma, prodorsum removed to show podocephalic gland ducts and tracheae. Parts overlying peritreme and podocephalic canal not shown on left; right tracheae (tri, trs) displaced for clarity. B. — Lateral (slightly anterior) view of anterior part of propodosoma, showing peritreme and proximal part of podocephalic canal (chelicerae and anterior podocephalic gland ducts not shown). C. — Lateral view of right gland duct dg5.

Abbreviations: CH chelicera; ap1 apodeme of epimere 1; cpc podocephalic canal; dg gland ducts; f fold over podocephalic canal; per peritreme; tri inferior trachea; trs superior trachea; sti inferior stigma; stre paraxial stigma; t tendons; tl tracheoles; Δ anterior epimeral condyle.
FIG. 4: Neoteneriflola coineai n. sp., genitalia.

A. — Female, lateral view of everted ovipositor (distal towards right); muscles (broken lines) only shown in part; dotted lines indicate unidentified tissues. B. — Female, posterior view of posterior lobe of ovipositor. C. — Female, ventrolateral view of genital papillae and eugenital setae $k_{1,3}$. D. — Male genitalia, ventral view. E. — Male genital area.

Abbreviations: $Ja$, $Jp$ anterior and posterior progenital comissures; $m$ muscles; $OP$ presumed oviduct; $Va$, $Vm$, $Vp$ anterior, median and posterior genital papillae.
Peritremes and tracheae (fig. 3B). — The peritremes begin above the anterodorsal margin of coxa I as variable, external, alveolar taenidia, alveoli arranged in two rows, which soon become invaginated (peritreme proper). Peritremes pass over bases of the chelicerae and descend to the ventral, paraxial stigmata (sttr). Stigma sttr is poorly defined, being simply the point at which the peritreme becomes closed (at the level of the ventral margin of the chelicera). Antiaxiad of sttr lies a second stigma, stti, which opens on the ventral face of the chelicera. This stigma is composed of a thin membrane which broadens towards opening (figs. 3A, B); the exact form of the opening could not be discerned, though it appears to be a simple slit. The dorsal trachea (trtr) is larger and has a thicker cuticle than that of the ventral trachea (trti). Both tracheae long, ramifying irregularly into tracheoles, those of trtr being more numerous. Tracheae trti and trtr soon join to form a common atrium, after which they separate. Trachea trti traces a single, long spiral around trtr, starting below it, in front of the atrium, then passing dorsally, paraxially and finally ending below it posteriorly. It lies close to trtr along the whole of its length (the tracheae have been artificially separated in figure 3A).

Podocephalic canal and gland ducts (fig. 3). — Podocephalic canal external for the whole of its length, but it is hidden anteriorly by a dorsal fold and passes between the rim of coxa I and the side of the body posteriorly. Five pairs of gland ducts open into canal: dt long and thin, reaching below tracheae, dg1 small, dg2 broad and intermediate in length between dt and dg1; ducts dt, dg1 and dg2 close together, opening above anterior border of infracapitular apodeme; duct dg3 small, lying above broad duct (dga) of coxal gland.

Gnathosoma: — Mouth bordered by three lips (labrum and paired lateral lips). Labrum small, dorsal surface ornamented with rows of very fine denticles, and bearing an anteriorly-directed projection near the middle; lacking a distinct sclerite, but with muscles attached posteriorly. Lateral lips small, distal paraxial surface with small lanciniae. Pharynx large, with irregular, transverse ridges on ventral surface; oesophagus simple. Infracapitulum with 4 pairs of setae: calcars (or1 and or2) short and blunt; both lateral and posterior setae long and acuminate. Supracoxal spine (e) short, showing slight signs of becoming sunken.

Epimera (figs 4A, B). — Coxal formula 4-3-4-3 (epimeral formula 4-3-4-4: the long, paired setae anterior to the aggenital series are considered here to represent epimeral setae 4a). Internally, between posterior epimera, lies a remarkably enlarged, thin, plate-like, sagittal apodeme (as), to which the leg muscles are attached; epimera II extended posteriorly, being fused medially to support apodeme as. Epimera I, III and IV recurved, but not meeting in midline. Epimeral apodemes strong. Sejugal region slightly bulging laterally. Supracoxal spine e1 present on coxa I, similar to e.

Female genitalia. — An extended ovipositor was found in a single gravid female (fig. 4A). It is generally similar to the ovipositors described in other Prostigmata, being relatively large and having the eugenital setae located near the base. It was flexed near the middle, the ventral half being directed anteriorly, giving it an L-shape. As this flexure was maintained after clearing in lactic acid it seems that this shape is normal and not an artifact of preservation. The ovipositor appears to be a simple, open tube: no indication of a tri-lobed opening could be recognized. The eugenital setae are hollow (eupathidial?); those of the ovipositor are arranged into two groups: an anterior group of three paired setae (ψ), and a posterior group of four pairs (ς) situated on a pair of small, posteroiolateral tubercles (fig. 4b). Three pairs of discoid genital papillae present, anterior pair slightly separated from the other two. Setae k1,3 each situated behind a papilla (fig. 4c).

Male genitalia. — Internal parts complex and strongly chitinous. Genital papillae and setae k1,3 as in female, except that k1 and Va are further apart from k2 and Vm. Other eugenital setae also hollow, showing a striking variety of forms. As the homologies between these and the eugenital setae of other Prostigmata are unclear, they are given numeric designations here (cf. fig. 7D). Anterior setae 1-3 acuminate, seta l without an obvious areole; seta 4 weakly barbed; seta 5 remarkably long, reaching
FIG. 5: Neoteneriffiola coinemi n. sp., female, right leg I.

level of seta 8 posteriorly, apparently with a single barb; seta 6 bifid, basal ramus simple, apical branch dividing into a brush-like plume of cilia; setae 7 and 8 directed vertically downwards, 8 simple and situated just antiaxiad of 7; seta 9 barbed, directed ventrally.

Chelicerae (figs 1A, 2A-D). — Typical, elongate and only moderately retractile; setae smooth, relatively short — chb not reaching end of chelicera. Base of each chelicera with a paraxial depression, together forming a slight cavity beneath the naso when chelicerae are retracted; ventral cuticle thin and slightly concave; dorsal surface with longitudinal striation; fixed jaw absent, replaced by a large, membranous oncophyysis (hyaline process); tip of chelicera bears a dorsal hollow tube, possibly the duct of a gland, opening through the oncophyysis as a styliform process (cs). Dorsal surface of movable jaw strongly concave. No cheliceral lyrifissure found. When at rest, the ends of the chelicerae lie between the lateral lips.

Palp (fig. 1b). — Raptorial, cuticle thick. Trochanter short and broad. Femur robust (particularly in larger females) ventrally divided by a desclerotized longitudinal suture; a long, acuminate seta present ventrodistally and a long, barbed seta dorsally. Genu with a long, acuminate ventral seta. Tibia with one barbed seta and three calcars.

**Fig. 6**: *Neoteneriffiola coineaui* n. sp., male, right leg I.
A-C. — Dorsal view of (A) Tarsus and apotele, (B) Tibia, (C) Genu. D. — Paraxial view of distal end of tarsus and apotele. (Figures A-C to same scale.)
Fig. 7: Neoteneriffiola coincaui n. sp., female, leg IV.
which bear fine keels ending in blunt points. Tarsus reduced to an oval plate, though still retaining articular muscles posteriorly; 9 phaneres present: 1 small solenidion (ω), 4 ordinary setae (designated 2, 4, 5, 6) and 4 eupathidia (designated 1, 3, 7, 8); differentiation of eupathidia similar to that of pedal eupathidia; eupathidium 2 coupled with seta 3, their areoles being contiguous.

Legs. — Long, descending order of leg lengths: IV-III-II-I. Lateral claws of legs bipectinate (most strongly on legs I-II); a small median claw present on posterior legs (figs 8A-D), absent on anterior legs. Lyrifissure present at base of tarsi I-IV, but difficult to see, as it lies at the border of the segment near the point of articulation with the tibia.

A curious feature of the legs is the unequal thickness of the cuticle of each segment. This is illustrated by the semi-schematic cross section of genu IV shown in fig. 7E. In general the cuticle decreases in thickness towards the ventral (slightly posterior) side, from the basifemur onwards.

Trichobotrial sensillum finely cilliated. Bothridium deep and weakly ridged around circumference (fig. 8E, F).

Setae similar in form to dorsal idiosomal setae, but tending to become smooth on venter of distal segments. Chaetotaxy relatively simple, with a maximum of five files [d, (l), (ν)] per segment. Numbers of setae in adult given in table 1.

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Table 1: Setae of adult leg segments

Seta k" (fig. 5G, H) present on tibia I, short, apically pyriform, only weakly birefringent at base. Famuli absent. Setae of legs I and IV and their partial development as shown in figures 5-7. Leg II similar to leg I except that: k" is absent from tibia; the basifemur bears an additional seta, ν'; d is absent from the genu; and seta d of the tarsus is normal (not eupathidial). Leg III differs from leg IV in having: ν" present on trochanter before n3; basifemur with ν"n3 present, d and l' appear before n3; tibia with l'n3, ν"n3, d(Ad) (and more distally placed); d(Ad) present subapically on telotarsus, and p eupathidial. The eupathidia are thin and finely ciliated (ciliation similar to that of trichobotria), with a lanceolate tip (fig. 5 F). Dorsal setae advance distally along the segment on becoming eupathidial.

The pedal solenidia can be divided into two groups:

1) The primary (orthotaxic) solenidia, comprising: ϕ1,2 of tibiae I, III and IV; ϕ1 of tibia II; ω1-4 of tarsi I-II; and ω1,3 of tarsi III-IV. The distal solenidion (ω1) of tarsi I-II is large, baculiform and erect, with a raised base (fig. 6D). The remaining orthotaxic solenidia are long, fine, upright and gently curved (figs 6A-C). Their tips are blunt, like those of the neotrichous solenidia of the nymphs and females, but they appear relatively more acuminate because of their greater size. The tibiae of the deutonymph bear ϕ1,2; ϕ2 is additionally present on tarsus III; ϕ3 IV is added in the tritonymph and ϕ2 I in the adult (it is absent from tibia II). Solenidion ω1 is present on tarsi I-IV of the deutonymph; ω3 I, ω2 III and ω2 IV appear in the tritonymph, whilst ω4 I-II and ω3 II-IV appear in the adult. Males sometimes bear a fifth primary-type solenidion just proximad of ω3, possibly due to a doubling of the latter.

2) The secondary (neotrichous) solenidia of the genu, tibiae and tarsi. In the nymphs and female, these are very small, thin, straight and blunt-tipped. The secondary solenidia of the male are large, curved (sometimes slightly S-shaped), baculiform and usually recumbent. Secondary solenidia are present on genua I-III in the deutonymph, whilst those of genu IV, the tibiae and the tarsi first appear in the tritonymph (those of tarsus IV are vertitional and may first appear in the adult). The numbers and positions of the secondary solenidia are highly variable, though there is a clear tendency for them to be arranged in two longitudinal rows as they increase in number. The total numbers for each segment are given in table 2.
Fig. 8: Neotenerifliola coineaui n. sp., female, tarsus IV.


Abbreviations: bas body of apotele; bpt posterior limit of pretarsus; cot cotyloid cavity; kph condylophore; nt terminal notch of basitarsus; oc median claw; ol lateral claw; ti inferior tendon, ts superior tendon of apotele.
The largest number of secondary solenidia on male tarsus I came from a single male which had 14 on the left tarsus I and 21 on the right, which may be exceptional. Another male had two solenidia arising one in front of the other from a single areole, though their bases were completely separate, on left tibia III.

Lengths of segments (measurements of male, followed by female in parentheses):

- **Leg I:** trochanter 165 (180); femur I 210 (220); femur II 170 (190); genu 250 (250); tibia 410 (365); tarsus 415 (380); total 1620 (1585).
- **Leg II:** trochanter 165 (200); femur I 215 (225); femur II 165 (180); genu 245 (215); tibia 420 (380); tarsus 400 (375); total 1610 (1575).
- **Leg III:** trochanter 165 (205); femur I 210 (190); femur II 165 (180); genu 255 (255); tibia 485 (485); basitarsus 405 (400); telotarsus 160 (140); total 1845 (1855).
- **Leg IV:** trochanter 240 (250); femur I 240 (200); femur II 185 (195); genu 285 (265); tibia 550 (560); basitarsus 440 (435); telotarsus 150 (155); total 2090 (2060).

**Table 2:** Numbers of secondary solenidia on segments of legs

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<td>1-2</td>
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<tr>
<td>IV</td>
<td>6-8</td>
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<td>♂ I</td>
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<td>II</td>
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<td>III</td>
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<tr>
<td>IV</td>
<td>6-11</td>
<td>18-20</td>
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**DISCUSSION**

**Eyes**

The gross morphology of the lateral eyes is similar to that of *Tetranychus urticae*, described by McENroe (1969) and Mills (1974). As seems to be typical for the eyes of Prostigmata (and Sphaeroli-chidae — Grandjean, 1939), the lateral eyes of *N. coineaui* are heteromorphic. When viewed in reflected light, the anterior eyes appear dark red, whilst the posterior pair are white. This is due to a difference between the pigment grains beneath the lenses. The pigment of the posterior eyes readily dissolves in lactic acid, whilst that of the anterior pair is more resistant.

A median eye is recorded here for the first time in the Tenerifiidae. Luxton (1993) noted the presence of a pigment spot in the naso of *Tenerifia mortoni* (Luxton) (*n*.comb. 2), but did not mention a median eye as such. The median eye of *N. coineaui* (fig. 1F) is well developed, consisting of a distinct lens on the venter of the naso and a ring of sparse pigment granules above it, which appear white in reflected light. The pigment ring is usually situated somewhat behind the lens, but it is unclear whether this represents the normal condition or an artifact of fixation/clearing. Despite the complete effacement of any trace of division, the organization of the median eye of *N. coineaui* is evidently of a primitive type, comparable to that found in some Bdellidae (Alberti, 1975).

**Trichobothria**

Although they have been shown in previously published figures of the prodorsum, the trichobothrial nature of *sa* seems to have gone unnoticed, though Eller & Strandtmann (1963) observed that they arise from “large pores”. This may be due to the fact that the bothridium is smaller than that of *sp* and lacks the obvious “rosette” of the latter. The anterior trichobothria are probably present in all Tenerifiidae.

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2. The genus *Heteroteneriffla* Hirst was synonymized with *Tenerifia* Thor by McDaniel et al. (1976). As Luxton (1993) makes no reference to that paper, I assume that he overlooked this synonymy and hence did not intend to revalidate *Heteroteneriffla.*
The rosette structure at the base of the posterior trichobothrium (sp) has been recorded and figured by most authors, but has only been treated in a superficial manner. The rosette consists of a variable number of cuticular tubes which open into the dorsal bothridial cavity, just below the outer rim. The cuticle of the vesicles is relatively thick and their peripheral ends are closed. They are similar to the single vesicles which open into the cavity of trichobothrium bo in the caeculid Procaeculus (COINEAU, 1974) and the palaeacaroid Acaronychus (GRANDJEAN, 1954). Multiple vesicles (logettes) of the bothridia of eupticine oribatids have been described by GRANDJEAN (1967). GRANDJEAN suggested that these logettes could be precursors of brachytracheae, though they are not themselves respiratory. Similarly, the cuticle of the vesicles of N. coineaui seems too thick for them to have a respiratory function.

Peritremes and tracheae

The tracheal system of Teneriffiidae is topologically X-shaped, with the node representing the atrium, a form shared with the Tetranychidae (ANDRÉ & REMACLE, 1984). This represents an intermediate condition between the presence of two separate pairs of tracheae and stigmata, found in the tydeid genus Tydaeolus for example, and that of the bdellid genera Odontoscirus and Neomolgus (GRANDJEAN, 1938a, 1938b) in which the single trachea on each side branches into the two stigmata anteriorly, giving it a Y-shape. The significance of the tracheal arrangement in teneriffiids is not clear, but it raises the question of whether there is an active circulation of gases during respiration. A fast moving mite the size of N. coineaui will obviously have relatively high respiratory requirements and it is possible that movements of the chelicerae serve to open and close stigmata sti.

Podocephalic canal and glands

The position and form of the glands of the podocephalic canal are similar to the condition described by COINEAU (1974, 1980) in the Caeculidae. As he pointed out, the presence of five pairs of gland ducts emptying into the podocephalic canal is unusual: only four pairs of podocephalic glands have been recorded in other Prostigmata (ALBERTI, 1973 — Bdellidae; ALBERTI & STORCH, 1973 — Tetranychidae; EHRNSBERGER, 1979 — Rhagidiidae; WITTE, 1978 — Erythraeidae). COINEAU suggested that the first pair of ducts of caeculids could be homologous with the infracapitular glands (dt) found in bdellids, but was reluctant to establish this homology in the absence of histological studies of the glands of caeculids, proposing instead the provisional notation dgπ. However, homologous glands of the podocephalic system have been shown to differ in form and function between groups (EHRNSBERGER, 1979) and it is unlikely that histological studies alone of Caeculidae and Teneriffiidae could either confirm or refute the hypothesized homology between dt and dgπ.

If ducts dt and dgπ are equivalent, no mite will have both at the same time. The discovery of five pairs of podocephalic gland ducts in teneriffiids, which lack infracapitular glands, provides support for their homology. It is worth noting that apparently intermediate conditions have been described in some families. In the Erythraeidae dt opens close to the distal end of the podocephalic canal in Abrolophus, whilst they are much further apart in Erythraeus (WITTE, 1978). GRANDJEAN (1943b) found a remarkable raised canal, connecting the podocephalic canal with the openings of dt and continuing to the base of the labrum, in Pachygna­thus (Alycidae). Given the presence of intermediate conditions in other taxa and the fact that dt and dgπ have never been found together, the notation dt is employed here for the first pair of ducts in Teneriffiidae.

The presence of a gland duct (dg5) opening above the coxae in the sejugal region of teneriffiids is particularly notable. This duct is evidently homologous with the 'Lassenia-organ' described in the Johnstanianidae and Trombidiidae (Parasitengona) by NEWELL (1957, 1958) and gland gl.c of coxa III found in the Caeculidae (COINEAU, 1963, 1974). It is also present in Anystis (pers. obs.), and it seems likely that it has a much wider systematic distribution than hitherto suspected.

GRANDJEAN (1968) and COINEAU (1974) interpr-
ted the infracapitular and podocephalic glands as forming a metameric series. Whether or not this is the case, it is evident that the gland ducts can vary in position relative to the primitive segmentation. The metameric notations employed by Grandjean (1971) and Coineau (1974) assumed that some of the glands \( g_1 \) and \( g_3 \) were composite. The histological studies of Alberti (1973), Alberti & Storch (1973), Ehrenberger (1979) and Witte (1978) show that these glands are separate and have different functions. Alberti (1973) presented a table of the equivalent terms used by different authors for the podocephalic glands and ducts. An additional table is given below, indicating the corresponding terms used by Alberti (1973), Coineau (1974) and those employed here for the gland ducts:

<table>
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<tbody>
<tr>
<td>dt</td>
<td>dglx</td>
<td>dt</td>
</tr>
<tr>
<td>d1</td>
<td>dglx</td>
<td>dgl</td>
</tr>
<tr>
<td>d2</td>
<td>dgl2</td>
<td>dgl2</td>
</tr>
<tr>
<td>d3</td>
<td>dgl3</td>
<td>dgl3</td>
</tr>
<tr>
<td>d4</td>
<td>dgl3'</td>
<td>dgl4</td>
</tr>
<tr>
<td>gI.c III</td>
<td>dgl5</td>
<td></td>
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</tbody>
</table>

Genitalia

In common with other Anystoidea, the cuticular genitalia of the male are complex, suggesting sperm transmission via an elaborate spermatophore (as has been demonstrated in Anystidae (Schuster & Schuster, 1966). The sexual dimorphism of the pedal solenidia of N. coineaui, suggests that spermatophore deposition, in this species at least, may be preceded by some form of mating dance.

The remarkable modifications of the eugenital setae of the male Tenerifiidae promise to provide useful systematic characters in this group. McDaniels, et al. (1976) illustrated hypertrophied eugenital setae, which they called 'genital claspers', in Teneriffia mexicana McDaniels, et al. and 'Parateneriffia' uta (Tibbetts). These indicate marked differences between species and this is confirmed by the examination of material of Neoteneriffiola and Teneriffia species (pers. obs.). The form of the female genitalia is also likely to be of value in the systematics of Prostigmata, though perhaps at higher taxonomic levels than that of the male. The basal position of the eugenital setae of the ovipositor in Prostigmata contrasts with that of oribatids, in which they are situated terminally on well-defined eugenital lobes.

Eller & Strandmann (1963) were of the opinion that the presence or absence of genital papillae stated by previous authors was due to a sexual difference, as they had found them in the female of 'Parateneriffia' uta, but not in the male. McDaniel et al. (1976), in their redescription of the same species, reported that the genital papillae were absent in the protonymph, deutonymph and male; that they "may be present" in the tritonymph; and that there were three pairs in the female. The development of the papillae in N. coineaui is normal, with two pairs in the deutonymph and three pairs in the tritonymph and adults (both sexes). It seems probable that the supposed deviations from the Oudemans-Grandjean rule are due to the difficulties involved in observing the rather obscure papillae of Tenerifiidae.

Putative cheliceral gland

A typical feature of tenerifiids is the presence of a cuticular stylet on the hyaline process (oncophysis) of the chelicera, situated paraxiad of the movable jaw. This structure continues internally as a duct, which is directed upwards to lie beside the dorsal part of the apotele (figs 2B-D). This organ is tentatively identified as the duct of a cheliceral gland (cg), though no trace of a gland has been detected in lactic acid preparations.

Cheliceral glands have been recorded sporadically in the Prostigmata (Evans, 1992) and may also occur in Opilioacarida (Hammen 1966). Moss (1962) identified the cheliceral gland of Trombididae as a probable venom gland.

Oncophysis of palp

The curious process found on the palpal tibia of all Tenerifiidae except Teneriffia, was first described by Thor (1911) and has been used as an important taxonomic character. The use of the term 'thumb' by some authors is unfortunate because it suggests that this structure is the equivalent of the
thumb (usually comprising one or two hypertrophied setae or calcars) of the 'thumb-claw complex' found in many prostigmatic groups. Examination of this process in polarized light shows that it is not a modified seta. Rather, it is a membranous swelling at the end of the genu, apparently derived from the arthrodial membrane between this segment and the tibia of the palp (fig. ID). In preserved specimens the membrane is slightly flattened laterally, but it expands when cleared in lactic acid, giving it a bulb shape. A rod of clear cuticle is present within the process, as figured by THOR (1911: fig. 6) in P. bipectinata. This sclerite (ops) is a continuation of the internal cuticle of the genu.

No homologous structure seems to be known in any other group of mites. The only organ which could be regarded as analogous is Trägårdh's organ, found in some oribatid groups. Trägårdh's organ is a continuation of the cheliceral sheath, containing an internal sclerite, which lead HAMMEN (1968) to suggest that it may be a modified oncophysis3. Given the structure of the thumb of Teneriffiidae, and its similarity to Trägårdh's organ, I propose to call it the palpal oncophysis (op). It is possible that the palpal oncophysis plays a mechanical role in holding prey, in a way similar to that suggested by GRANDJEAN (1959) for Trägårdh's organ.

Phanerotaxy of the legs

The setae of files (l) and (v) are regularly placed and show little variation in N. coineaui. GRANDJEAN (1943a) argued that the similarly uniform pedal chaetotaxy of the larva of Anystis represents a primitive type. However, one could argue that the converse is true — that the arrangement of the setae in Teneriffiidae and Anystis is derived. The simplicity of the basic pedal chaetotaxy in these and other long-legged taxa is probably due to the fact that most of the segments are well apart from both the body and each other and are therefore unencumbered. Whether the setal pattern is primitive or secondary depends on whether they are derived from mites with long or short legs.

The distal displacement of dorsal setae on becoming eupathidial agrees with GRANDJEAN'S (1943a) and COINEAU'S (1974) observations of this phenomenon in other Prostigmata.

The oblique alignments of the lateral setae, particularly on the genua, are similar to those found in Anystis. GRANDJEAN (1943a) initially considered that the lateral setae of the larva of Anystis represented two files (l and e), but later revised this opinion in the light of his studies of erythraeoids, supressing ep in favour of lp for segments other than the basifemur and tarsus, where some doubt remained. The chaetotaxies of the Caeculidae and Teneriffiidae, in which the files are even clearer, confirm GRANDJEAN'S corrections and indicate that they should be extended to include the tarsi.

The identity of seta bv" of the basifemora I-II is problematic. In mite taxa in which the femora are undivided, the notation bv" is employed to indicate a seta which belongs to the primitive basifemoral segment. Although the femora of teneriffiids are completely divided, the apparent posterior ventral file is heteronomic: the basal seta (bv") appears before v" during development. The presence in Teneriffia of a complete verticil of five setae, along with bv", on basifemora of leg II, indicates that this seta has not migrated from a posteriolateral position. The notation bv" is used for the basal femoral seta of teneriffiids, partly to indicate positional and ontogenetic similarities to setae bv" in other mites, and partly to indicate its uncertain identity.

The neotrichous solenidia show a marked tendency to form two longitudinal rows, but do not behave as files during ontogeny. It is for this reason that they are described as being neotrichous, rather than cosmiotrichous, here. The neotrichy of the solenidia in N. coineaui poses some interesting questions which can only be dealt with once the development of this and other species is known in detail. A comparison with the solenidiotaxy of Pachygnathus (GRANDJEAN, 1942) will probably be instructive.

3. The term 'oncophysis' was introduced by HAMMEN (1968) to describe membranous swellings (bouffissures paraxiales) of the arthrodial membrane of the chelicerae of oribatids and Erythraeoids (GRANDJEAN 1947, 1959). As HAMMEN's definition is not restricted to structures found on the chelicera, the term is used here for this analogous structure on the palp of teneriffiids.
Apoteles and secondary tarsal joints of posterior legs

Teneriffiidae are known to be fast-moving animals (Hirst, 1926; Coineau, pers. comm.). In common with other fast-running mites, they show elongation of the legs and the development of increased flexibility, particularly of the posterior pair. One of the most characteristic features of the Teneriffiidae is the secondary division of tarsi III and IV into two, secondary segments — the basitarsus and telotarsus. This character been cited in all previous diagnoses of the family, but the exact nature of the articulation has remained undescribed. The articulation between the basi- and telotarsus of these legs (figs. 8E, F) has a strange appearance, seeming to be the 'wrong-way-round' at first sight. This is because the articulation is constructed to allow the dorsal displacement of the telotarsus relative to the basitarsus, thus moving in the opposite direction to the other segments of the leg. There are no condyles and the telotarsus is capable of a wide degree of movement in both horizontal and vertical planes. Flexure of the telotarsus tends to push the base against the tendons of the apotele and it may be that, in addition to the elasticity of the joint, the tension created in the tendons helps to return the telotarsus to its 'normal' position. The upper displacement of the tendons is limited by a dorsal thickening of the cuticle at the base of the telotarsus (fig. 8E).

The uneven thickness observed in the cuticle of the legs might also be related to fast running. The thickened dorsal surfaces of the segments may correspond to regions of greatest stress during running. Most of the increased thickness appears to be due to the presence of a thicker layer of endocuticle, which is more elastic than the exocuticle.

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