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Review of the Upside-down Flies (Diptera: Neurochaetidae) of Madagascar and Africa, and Evolution of Neurochaetid Host Plant Associations

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ABSTRACT. The subgenera *Neurocytta* McAlpine and *Neurotexis* McAlpine are raised to genera. A revised key to genera of recent Neurochaetidae and a key to species of *Neurotexis* are given. The new species *Neurotexis maura, N. despiciens, N. termon, N. kaplanae, N. delphis, N. charis, N. primula, N. vesca, N. freidbergi* and *N. polyaster*, all from Madagascar, are described. *Neurocytta prisca* (McAlpine) and *Neurotexis stuckenbergi* (McAlpine) are new combinations (from *Neurochaeta*). Additional morphological details are given for *Neurocytta prisca.* Morphology of the neurochaetid antenna is reviewed. Head-downwards cursorial behaviour is recorded for almost all known Afrotropical species. Apparent host plants recorded for 11 of these are *Strelitzia* and *Ravenala* (Zingiberales: Strelitziaceae) and *Pandanus* (Pandanales: Pandanaceae). Host plant records are superimposed on a revised cladogram of neurochaetid species in an attempt to trace out evolutionary changes in fly-plant associations. An early zingiberalean plant possibly provided the plesiotypic host plant association for Neurochaetidae, and there is evidence that such a plant may have been available to the early Tertiary neurochaetid *Anthoclusia.*

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The family Neurochaetidae has been only recently described (McAlpine, 1978) and, when the family was last revised (McAlpine, 1988a, 1988b), the Afrotropical representatives were still only known from three preserved specimens. Significant new material was obtained through recent field work in Madagascar and Zimbabwe by A. Freidberg, F. Kaplan, and the author. It is probable that additional Afrotropical species await discovery, but with more than 300 specimens available, I am able to record a significant increase in knowledge of the fauna.

Previously (McAlpine, 1988a) I separated the two imperfectly known Afrotropical species as two monotypic subgenera of *Neurochaeta* McAlpine, preferring caution in view of the slight knowledge of this fauna. With the ten new species here described, it is clear that the Madagascar species form a well-defined monophyletic group with some diversity, comparable with *Neurochaeta* s.str. of the Oriental and Australian regions, also that the only known African species is phylogenetically removed from both the above groups.

The forecast of Woodley (1982) that separate genera (from *Neurochaeta*) might eventually be needed for *N. prisca* and *N. stuckenbergi* is now fulfilled, *Neurocytta* McAlpine and *Neurotexis* McAlpine being elevated to generic status.

The head-downwards cursorial behaviour responsible for the appellation 'upside-down fly', has been shown to be general for *Neurochaeta* s.str. (McAlpine, 1988b), but new observations demonstrate its presence also in species of *Neurocytta* and *Neurotexis*. The similarity of *Neurocytta* to the Tertiary stem-group *Anthoclusia* Hennig suggests that the latter may have possessed similar cursorial behaviour.

Morphological terminology here follows that of Harrison (1959) with particular morphology for Neurochaetidae as given by McAlpine (1988a).

The names of the following collectors are abbreviated to the initials: A. Freidberg, F. Kaplan, D.K. McAlpine.

Institutions housing specimens are abbreviated as follows: AM – Australian Museum, Sydney; BM – British Museum (Natural History), London; CNC – Canadian National Collection, Agriculture Canada, Ottawa; MNM – Hungarian National Museum, Budapest; NAT – Natal Museum, Pietermaritzburg; PM – National Museum of Natural History, Paris; TAU – George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv; USNM – National Museum of Natural History, Washington.

Key to Recent Genera of Neurochaetidae

1. Eye with coarse ommatrichia; costa unbroken; alula without fringe; functional tarsal claws absent (Australia) ..... *Nothoasteia*

—— Eye with at most few, minute ommatrichia; costa with break at end of subcosta; alula with marginal fringe; tarsal claws developed 2

2. Arista short-plumose, its longer rays less than 0.2 length of arista; scutellar bristles of major pair approximated near apex; subscutellum little developed (Fig.1B); second basal cell complete (Africa) ..... *Neurocytta*

—— Arista long-plumose, its longer rays more than 0.3 length of arista; scutellar bristles of major pair widely separated; subscutellum enlarged, encroaching on postscutellum (Fig.1C); second basal cell incomplete 3

3. Second basal cell confluent with discal cell; costa terminating at vein 3; radial sector without bristles; posterior margin of scutellum bare between major bristles (Madagascar) ..... *Neurotexis*

—— Second basal cell confluent with first basal cell; costa terminating at vein 4; radial sector dorsally towards base with 2-4 strong erect bristles; posterior margin of scutellum with one or more pairs of shorter bristles between major pair (South East Asia to Australia) ..... *Neurochaeta*

Neurocytta McAlpine n.stat.

Neurocytta McAlpine 1988a: 43, 44 (as subgenus of *Neurochaeta*). Type species *Neurochaeta prisca* McAlpine.

Comments. This group remains monotypic and, though the diagnostic characters given previously are still valid, the frontal bristles and antennae of the previously available material were damaged. The following is a supplement to the previous subgeneric description on the basis of additional specimens.

Description. Fronto-orbital bristles 4, including 2 reclinate bristles (1 specimen with anterior reclinate bristle duplicated on both sides) and, anteriorly, 2 incurved bristles, 1 situated mesad of and slightly in advance of foremost reclinate bristle, and 1 situated well in advance of and somewhat less mesad of anterior reclinate bristle. Antennal segment 2 less enlarged and cucullate than in *Neurotexis* and *Neurochaeta*, with comb of setulae on outer distal margin very weakly developed, without a differentiated ventral bristle; arista with well developed, rotund, short-haired segment 5; segment 6 bipectinate, with rays no longer than diameter of segment 5. Prosternum oblong, with median groove and several marginal setulae on each side; metasternum setulose; scutellum and postscutellar parts, other than subscutellar

membrane, strongly dorsoventrally compressed; subscutellum little developed, narrowed medially, not encroaching on the much deeper postscutellum.

Notes. I have previously (McAlpine, 1978, 1988a) mentioned several characters in which *Neurocytta prisca* resembles the Baltic amber fossil *Anthoclusia* Hennig (particularly *A. gephyrea* Hennig) rather than the other recent species of *Neurotexis* and *Neurochaeta*. Observations on the new material of *Neurocytta* confirm the plesiomorphic proportions of the subscutellum and postscutellum which would appear to resemble those of *Anthoclusia*, though both parts are reduced in depth in *Neurocytta*. The presence of two pairs of inclinate fronto-orbital bristles in *Neurocytta* is also in agreement with *Anthoclusia* (see particularly Hennig 1967), though in *Neurocytta* these are situated mesad of the line of the reclinate fronto-orbitals as in *Neurotexis* and *Neurochaeta*. The antenna of *Neurocytta* resembles that of *Anthoclusia* and differs from that of *Neurotexis* and *Neurochaeta* in having a less developed segment 2 without a differentiated ventral bristle, and in having the arista (segment 6) with relatively numerous quite short dorsal and ventral rays. *Anthoclusia remotinervis* Hennig differs from *A. gephyrea* Hennig in having the lateral scutellar bristle replaced by two or three small setulae ("Härchen"), a condition approaching that of *Neurocytta*. *Neurocytta* also agrees with *Anthoclusia* and differs from some other living neurochaetids in the presence of a distal anteroventral comb on the fore femur.

While I do not believe that there is adequate evidence to demonstrate that the known species of *Anthoclusia* can be assigned to separate lineages ancestral to various living neurochaetids, it is interesting to note that some of the present diversity of modern neurochaetids was represented in this early Tertiary fauna. The supplementary observations on *Neurocytta*, given above, confirm its status as an interesting link between the fossil forms of *Anthoclusia* and the living *Neurochaeta* and *Neurotexis*.

Neurocytta prisca (McAlpine) n.comb.

Figs 1, 8

Neurochaeta prisca McAlpine, 1978: 282-283, figs 9-11, 21.

Additional material examined. 4 females, 'Banana Grove', Chimanimani (formerly Melsetter) National Park, 23 Sept. 1990, D.K.M. (AM, USNM).

Distribution. Zimbabwe (formerly Southern Rhodesia) – mountains of eastern border district. The distribution is probably limited by availability of *Strelitzia* plants. The type locality is given as 'Melsetter', a village now called Chimanimani. *Strelitzia augusta* grows in the vicinity of Bridal Veil falls, about 3 km from the village. This may be the source of the type material, but, in my brief visit there, I did not find *N. prisca*. 'Banana Grove', where I collected my material, is about 22 km further east.

Notes. The previously given characterisation of the species is supplemented under the generic heading.

Neurotexis McAlpine n.stat.

Neurotexis McAlpine 1988a: 43, 44 (as subgenus of *Neurochaeta*). Type species *Neurochaeta stuckenbergi* McAlpine.

Comments. The diagnostic characters are essentially as given by me (1988a) for the monotypic subgenus *Neurotexis*, but, because several species have now been seen, the description must be modified.

Description. Fronto-orbital bristles normally 4, the inclinate one inserted mesad of and somewhat before to somewhat behind anterior reclinate one; postvertical

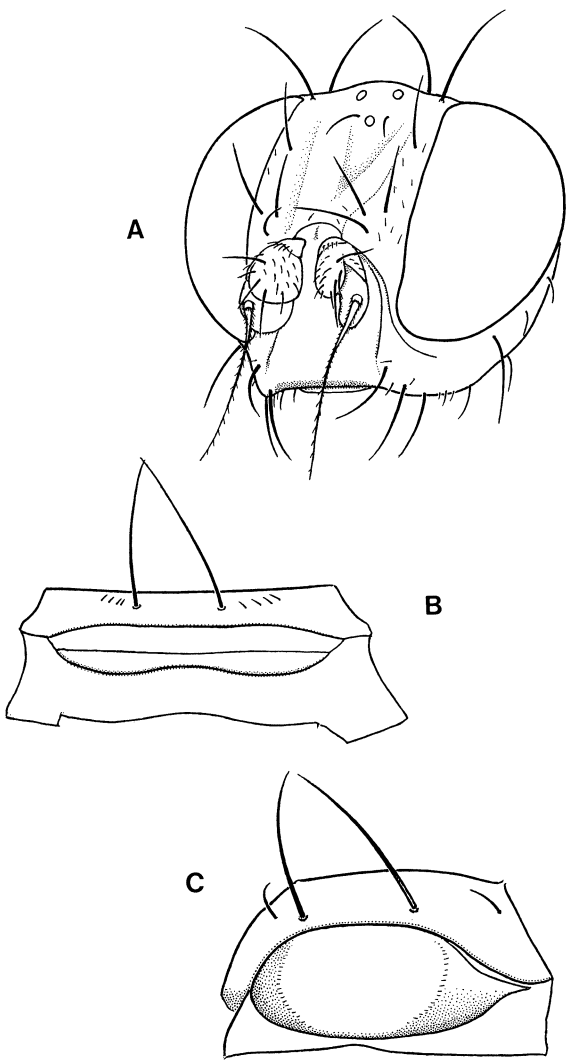

Fig.1. *Neurocytta prisca*. A, head; B, scutellum and postscutellar parts posterior aspect. *Neurotexis primula*: C, same parts.

bristle and one postgenal bristle present; suborbital bristle absent. Antenna: segment 2 large and cucullate, with ventral bristle usually long, its medial lobe with several thick bristles, outer lobe with a regular marginal series of pale setulae; segment 3 with group of enlarged apical microtrichia; segments 4 and 5 very small, pubescent, sclerotised; segment 6 long-plumose, with several long dorsal rays situated on basal swelling, beyond base with long dorsal and ventral and short medial rays. Presutural bristle present, sometimes vestigial; dorsocentral bristles 1 or 2; supra-alar bristles 1 or 2; scutellar bristles in 2 pairs: widely separated major pair, and shorter lateral pair; subscutellum deep, convexly prominent, usually with silvery pruinescent zone; mesopleuron devoid of setulae; sternopleuron with 1 or 2 upper posterior bristles, with or without short upper anterior bristles; prosternum and metasternum bare. Costa terminating immediately beyond end of vein 3, with spaced anteroventral bristles between terminations of veins 1 and 2, without erect dorsal setulae immediately before end of subcosta; costal section before subcostal break produced distally in front of break as a long, finger-like process (costal lappet), or only vestigial process present; radial sector without macrotrichia; distal section of vein 5 not shorter than penultimate section of vein 4; second basal cell separate from first basal cell, confluent with discal cell; anal cell small, often imperfectly enclosed; vein 6 often sclerotised for short distance beyond anal cell; alula rather narrow. Abdominal tergites 2 or 3 to 6 or 7 with bristle near each posterolateral angle. Postabdomen of male, where known, with well developed, asymmetrical sternites 6 and 7, and dorsal sternite 8; epandrium well developed, with 2 pairs of long bristles and articulated surstylus, which is not expanded into a basal plate; hypandrium with pair of large, almost flat plates each having 1 or 2 bristles, without process (outer gonite of McAlpine, 1988a) at lateral margin of each plate (present in *Neurochaeta* s.str.), but with well-developed, bristled posterior gonite (corresponding to inner gonite of *Neurochaeta*); basiphallus rather short, sclerotised, with strong posterior process (epiphallus); distiphallus long, coiled in repose like a watch spring, sclerotised only on 2 longitudinal strips; proctiger with pair of ridges, each with sclerotised strip along summit.

Notes. The presence of two posterior sternopleural bristles in some species of *Neurotexis* prevents the number of sternopleurals being used as an apomorphy in evidence for uniting *Neurotexis* and *Neurochaeta* as a monophyletic group (see Woodley, 1982; McAlpine, 1988a). However, this monophyly is further supported by the following apparent synapomorphies: antennal segment 2 enlarged; antennal segment 2 with one enlarged ventral bristle; rays of arista lengthened and reduced in number; subscutellum with shining silvery pruinescence.

Two features of the epandrium of male *Neurotexis* are highly characteristic and probably ground plan states for the genus, though they cannot be classed as autapomorphies for *Neurotexis* on present evidence. These are: epandrium with two pairs of enlarged bristles, and epandrium with zone of silvery pruinescence. In *Neurochaeta*, the sister group of *Neurotexis*, the greatly reduced epandrium (an autapomorphy for *Neurochaeta*) has, in some species, one or two pairs of bristles, so that an ancestral form may have shared the epandrial bristling occurring in *Neurotexis*. In view of the great reduction of the epandrium in *Neurochaeta*, any pruinescent zone, which an ancestor might have shared with ancestral *Neurotexis*, would probably have been lost.

The following distinctive apomorphies attest to the monophyly of the genus *Neurotexis* in its newly expanded scope: i) presutural bristle present; ii) costa terminating just beyond vein 3; iii) distal section of vein 4 largely desclerotised; iv) dorsal macrotrichia on radial sector absent; v) second basal cell confluent with discal cell.

Like *Neurochaeta* s.str., *Neurotexis* is now known to exhibit some morphological diversity. The two groupings shown in couplet 1 of the key to species and in Figure 9 are perhaps monophyletic. The *polyaster* group (*N. vesca, N. freidbergi, N. polyaster*) shows the following possible autapomorphies: frontal bristles shortened; scutellum shortened; 2 supra-alar bristles present; thorax strongly depressed. The *stuckenbergi* group shows the following probable autapomorphy: face strongly convex below. Polarity in the characters distinguishing these two groups has been determined by reference to the apparent ground-plan states for the genus *Neurochaeta* (the sister group of *Neurotexis*), and also to some extent by consideration of *Neurocytta* (the out-group next removed), and *Anthoclusia* (the approximate stem-group).

Within the *polyaster* group, monophyly of the clade *N. freidbergi* + *N. polyaster* is supported by the following apomophies: fronto-orbital plates broadened; anterior part of mesopleuron very strongly sloping mesad from upper margin to coxal cavity; abdominal tergites two to six with silvery-pruinescent desclerotised spots. The sister group of the above clade is the species *N. vesca*, with the following notable apomorphies: pigmentation much reduced; costal lappet vestigial.

Within the *stuckenbergi* group cladistic relationships are more difficult to determine. Male postabdominal characters are not among the most suitable characters for this analysis because they are inherently unstable above the species level (McAlpine, 1988b). The most significant remaining character sequences concern bristling and colouration. I identify three probable clades within the *stuckenbergi* group but do not believe I have sufficient evidence to demonstrate an ordered sequence between these.

1. The species *N. charis* alone is taken as the first clade. This has probably the most plesiomorphic development of the dorsocentral bristles as indicated by similarity to the apparent stem group *Anthoclusia*. *Neurotexis charis* is not so close to the other two clades as to suggest that either of the latter is a derivative from within existing populations of this species though individuals show more variation than is apparent for other *Neurotexis* species.

2. *Neurotexis primula* is considered to constitute a clade distinguished inter alia by reduction of dorsocentral bristles to one pair (probable apomorphy) and the robust, deep, dorsally convex thorax (perhaps a plesiomorphy or reversal by comparison with stem group *Anthoclusia*).

3. The species *N. delphis, N. stuckenbergi, N. kaplanae, N. maura, N. despiciens, and N. termon* form a group with the following distinctive apomorphy: mid femur with the proximal bristle of the anteroventral series enlarged. Otherwise these six species have greater development of the costal lappet than any other neurochaetids, a further possible synapomorphy, and agree in having the thorax slightly depressed and the dorsocentral bristles of similar proportions, character states not demonstrably apomorphic though differing from those of the other species of this group. The species *N. delphis* and *N. stuckenbergi* are doubtfully distinct from each other and are therefore provisionally treated as a unit. The remaining *Neurotexis* species *N. kaplanae, N. maura, N. despiciens* and *N. termon* perhaps form a monophyletic group, supported by the following possible synapomorphies as evidenced by outgroup comparison within the *stuckenbergi* group: thorax almost entirely darkly pigmented; surstylus with one or few heavy bristles. The three species *N. maura, N. despiciens* and *N. termon* perhaps form a monophyletic group supported by the following possible synapomorphy as evidenced by comparison with all outgroups in the *stuckenbergi* group: abdominal tergite 2 almost entirely blackish. The apparent sister group of the last three species is *N. kaplanae*, having tergite 2 bicoloured. Host associations are deliberately excluded from the phylogenetic evidence at this stage.

Key to the Species of *Neurotexis*

1. Two supra-alar bristles present; inclinate fronto-orbital bristle inserted anteriorly to foremost reclinate fronto-orbital; lower part of face not or little inflexed, its surface thus not facing ventrally (*polyaster* group) 2

—— One supra-alar bristle present; inclinate fronto-orbital bristle usually not anterior to foremost reclinate one; lower part of face strongly inflexed, thus partly facing ventrally (*stuckenbergi* group) 4

2. General colouration, including bristles, pale yellow; sclerotised fronto-orbital plate narrow, poorly demarcated; costal lappet very short ..... *Neurotexis vesca*

—— General colouration brown-black, with areas of silver-grey to yellow pruinescence and mostly black bristles; sclerotised fronto-orbital plate at least as broad as interfrontal zone, sharply demarcated; costal lappet elongate, defined by a deep incision 3

3. Face convex on lower half in profile; ground colour of interfrontal tawny below greyish pruinescence; pale pruinescence of mesoscutum yellowish, only silvery at sides; major scutellar bristle longer than scutellum ..... *Neurotexis freidbergi*

—— Face straight in profile; ground colour of interfrontal largely dark grey below paler pruinescence; pruinescence of mesoscutum silver-grey; major scutellar bristle shorter than scutellum ..... *Neurotexis polyaster*

4. Mesoscutum yellow, except at anterior extremity; dorsocentral bristles one pair ..... *Neurotexis primula*

—— Mesoscutum predominantly brown to black, with grey pruinescence or yellowish zones; dorsocentral bristles 2 pairs 5

5. Anterior dorsocentral bristle as long as distance between anterior and posterior dorsocentrals; mesoscutum sharply bicoloured, dark brown and yellow; scutellum blackish with pale apex; mid femur with proximal bristle of anteroventral series not enlarged ..... *Neurotexis charis*

—— Anterior dorsocentral bristle much shorter than distance between dorsocentrals; mesoscutum not sharply bicoloured, with fulvous zones, if present, largely obscured by grey pruinescence; scutellum entirely dark; mid femur with proximal bristle of anteroventral series enlarged 6

6. Bristles on antennal segment 2 yellow ..... *Neurotexis stuckenbergi*

—— Bristles on antennal segment 2 predominantly black 7

7. Sternopleuron pale fulvous; mesoscutum brown, usually with posterior fulvous zone more or less concealed by grey pruinescence ..... *Neurotexis delphis*

—— Sternopleuron usually uniformly brown; ground colour of mesoscutum usually entirely brown-black, but surface partly concealed by grey pruinescence 8

8. Terminal segment of mid and hind tarsi brown; male: hind femur with a series of ventral bristles extending well distad of midlength; surstylus swollen near middle of anterior margin, narrowed basally ..... *Neurotexis maura*

—— Terminal segment of mid and hind tarsi yellowish or faintly browned; male: hind femur with a series of ventral bristles confined to basal half or almost so; surstylus not narrowed basally 9

9. Abdominal tergite 2 yellowish on about anterior half, brown posteriorly; male: lateral margin of tergite 6 with at least one other bristle more than half as long as large bristle at posterolateral angle; distiphallus sub-basally on right side with elongate denticles about 4.0 µm long ..... *Neurotexis kaplanae*

—— Abdominal tergite 2 almost entirely dark brown; male: lateral margin of tergite 6 with no other bristle over half as long as major posterior one; sub-basal denticles on distiphallus shorter, conical or vestigal 10

10. Male: surstylus in lateral view not broadened basally, with simple apex, with largest bristle situated near or slightly beyond middle of inner surface and at least one third as long as surstylus ..... *Neurotexis despiciens*

—— Male: surstylus in lateral view broad basally and tapered towards midlength, its apex with concave depression on outer surface, bevelled on inner surface, with 2 bristles less than one quarter as long as surstylus at base of bevelled surface ..... *Neurotexis termon*

Neurotexis maura n.sp.

Fig.2

Material examined. HOLOTYPE male, Madagascar: Andasibe (Perinet), 15-16 May 1987, D.K.M. (AM). PARATYPES, 6 males, same data (AM, USNM). Other material (not types), 3 females, same data (AM, USNM).

Description. *Colouration.* Head and its appendages predominantly yellowish; postfrons and antenna tawny-yellow, the former greyish brown centrally; occiput largely blackish brown; cheek bristles yellowish brown to blackish; other major cephalic bristles dark brown to black. Mesoscutum and scutellum entirely brown-black, the former with grey pruinescence centrally and posteriorly; subscutellum with large silvery-white pruinescent central zone; sternopleuron brown-black except for small yellowish area near sternopleural bristle; humeral callus brown. Legs yellow; hind femur blackish on somewhat more than distal half; terminal segment of mid and hind tarsi brown. Wing membrane tinged with brown in costal region; alula brown. Haltere pale yellowish. Abdominal tergite 1 yellowish, tergites 2-6 almost entirely brown-black; in male sternites 3-5 brown-black, in female these sternites generally paler.

Head higher than long; postfrons almost as long as wide; face broadly convex on lower part; fronto-orbital bristles moderately long and strong, the inclinate one inserted slightly behind level of anterior reclinate one, but also somewhat reclinate; inner vertical bristle scarcely shorter than posterior fronto-orbital; postvertical bristles convergent or parallel; vibrissa succeeded by 4 well developed cheek bristles. Antenna with about 5 dorsal rays on basal swelling of segment 6, in addition to more distal dorsal and ventral rays.

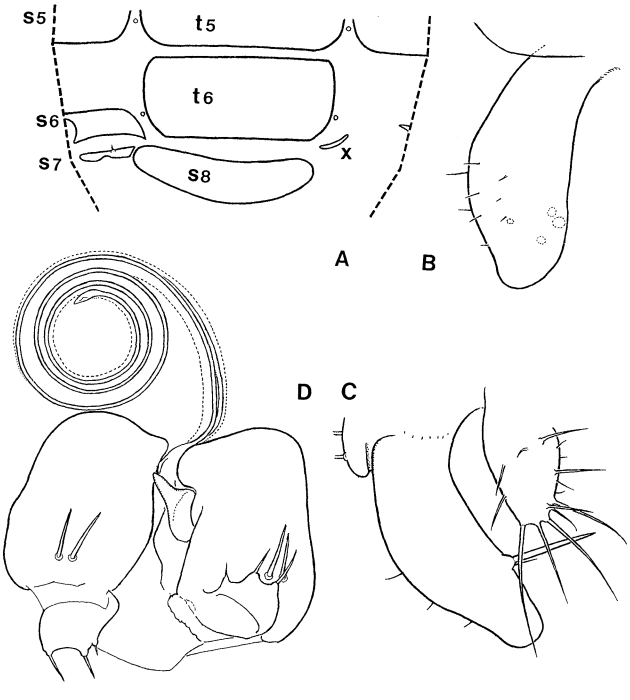

Fig.2. *Neurotexis maura.* A, protandrogram; B, left surstylus, outer aspect; C, left surstylus and cercus, posterior aspect: D, hypandrium and aedeagus. s5-s8 – sternites 5 to 8; t5-t6 – tergites 5 to 6; x – unidentified sclerite.

Thorax rather short, only slightly depressed; dorsocentral bristles 2, anterior one very short and far from posterior one; presutural bristle distinct but small; one supra-alar bristle present; major scutellar bristle much longer than scutellum; one long posterior sternopleural bristle present and sometimes a short one close in front of it. Legs of moderate dimensions; mid coxae well separated; fore femur with 5 or 6 well developed posteroventral bristles, a few weak anterior bristles towards base, and one or few dorsal bristles distally; mid femur with 2-4 anteroventral bristles, basal one much the largest; hind femur in male with a well developed series of ventral bristles which gradually decrease in size beyond middle, in female these bristles replaced by fine hairs; hind tibia with 2 short, thick anteroventral apical spurs, and, in male only, an acute, decurved posteroventral apical tooth. Costal lappet very strong, like that of *N. stuckenbergi*; anal crossvein indistinct; costal index 2.5-2.7; vein 4 index 5.8-7.1.

Abdomen. Male postabdomen: tergite 6 with about 3 lateral bristles of which no other member is more than half as long as posterior member; surstylus elongate, with largely flattened inner surface, with outer surface rather inflated, particularly near middle of length, with base a little narrowed in lateral aspect and overlapped anterolaterally by lobe of epandrium, with apex a little narrowed and compressed, with 2-4 bristles on inner surface beyond middle, of which one or 2 are quite large; each plate of hypandrium with 2 large bristles in front of gonite; gonite short and broad, with 3 bristles on distal margin, the inner one smaller; distiphallus with very few minute denticles on zone beyond base, larger ones about 1.5 μm long.

Dimensions. Total length, male 1.9-2.4 mm, female 2.0-2.4 mm; length of thorax, male 0.8-0.9 mm; female 0.8-0.9 mm; length of wing, male 1.9-2.0 mm, female 1.8-2.1 mm.

Distribution. Madagascar – central eastern district.

Notes. *Neurotexis maura* is among the darkest species of the *stuckenbergi* group, having both the mesoscutum and sternopleuron heavily pigmented. *Neurotexis despiciens, N. kaplanae,* and *N. termon* are similar in this respect, but *N. maura* has the terminal segment of the mid and hind tarsi more strongly browned than is usual in those species. Apart from this slight difference in tarsal colouration, I am only able to distinguish *N. maura* from *N. despiciens* and *N. termon* by male-restricted characters of which the most significant are given in the key to species.

Because *N. maura, N. despiciens*, and *N. termon* were all found on *Pandanus* at Andasibe at the same time, the females cannot be determined by apparent association with males, and no female paratypes are designated.

Etymology. The specific epithet is Latinised from the Greek adjective *mauros*, dark.

Neurotexis despiciens n.sp.

Fig.3

Material examined. HOLOTYPE male, Madagascar: Andasibe (Perinet), 15-16 May 1987, D.K.M. (AM). PARATYPE, 1 male, same data (USNM).

Description. Very similar to *N. maura*, agreeing with description of that species except as indicated below. Female unknown.

Colouration. Terminal segment of mid and hind tarsi indistinctly browned, faintly darker than rest of tarsi.

Thorax. Hind femur with a series of ventral bristles on basal part, rapidly decreasing in length about middle of length of femur and discontinued thereafter; hind tibia as in *N. maura*. Costal index 2.9-3.0; vein 4 index 5.2-5.6.

Abdomen. Male postabdomen: margin of epandrium with less developed lobe than in related species, only slightly overlapping base of surstylus; surstylus moderately elongate, slightly recurved, not incurved, compressed, so as to appear slender and straight in posterior aspect, broadly rounded apically, where it is convex on outer surface, planate on inner surface, near or a little beyond middle of length on posterior part of inner surface with large bristle more than one third as long as surstylus, anterior to this at same level a variable smaller bristle or setula; gonite with 2 bristles; aedeagus with a series of denticles on right side on zone beyond base, larger ones about 2-4 μm long.

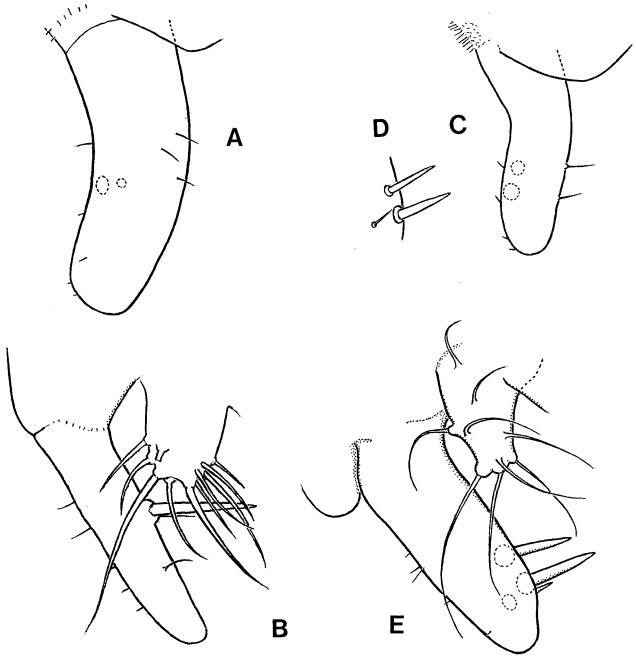

Fig.3. *Neurotexis despiciens*. A, right surstylus, outer aspect; B, left surstylus and cercus, posterior aspect. *Neurotexis kaplanae*. C, right surstylus, outer aspect; D, bristles of last at same scale; E, left surstylus and cercus, posterior oblique aspect.

Dimensions. Total length about 2.1 mm; length of thorax 0.8-0.9 mm; length of wing 1.8-1.9 mm.

Distribution. Madagascar – central eastern district.

Notes. *Neurotexis despiciens* is extremely similar to *N. maura, N. termon* and *N. kaplanae*, and is most reliably distinguished by the characters of male postabdomen given in the description and in the key. No females can be referred to the species at present and these should be difficult to distinguish from other species, particularly the sympatric, apparently host-sharing *N. termon*, unless the differences in wing indices prove consistent.

Etymology. The specific epithet is from the Latin participle *despiciens*, looking downwards, in reference to the usual orientation of the insect.

Neurotexis termon n.sp.

Fig.4

Material examined. HOLOTYPE male, Madagascar: Andasibe (Perinet), 15-16 May 1987, D.K.M. (AM). PARATYPES, 21 males same data (AM, BM, PM, TAU, USNM). Other material (not types): 20 females, same data (AM, USNM).

Description. Very similar to *N. maura*, agreeing with description of that species except as indicated below.

Colouration. Terminal segment of mid and hind tarsi slightly browned, most distinctly so on distal part of dorsal surface.

Thorax. Hind femur in male with a series of rather short stout ventral bristles on basal part, which is abruptly discontinued just before middle of length of femur; hind tibia as in *N. maura*. Costal index 2.7-3.2; vein 4 index 6.0-6.8.

Abdomen. Male postabdomen: surstylus in outer aspect slightly broadened basally, tapering thence towards middle, rounded apically, its outer surface at apex slightly concave, inner surface at apex bevelled or chisel-like, two often unequal bristles at base of bevelled surface, ie, much nearer apex than in related species; gonite more narrowed than in *N. maura*, with 2 stout bristles; distiphallus with a series of sharp, conical denticles along right side of sub-basal part, each about 3.0 μm long.

Dimensions. Total length, male 1.7-2.3 mm, female 1.1-2.2 mm; length of thorax, male 0.8-0.9 mm, female 0.8-0.9 mm; length of wing, male 1.8-1.9 mm, female 1.8-2.0 mm.

Distribution. Madagascar – central eastern district.

Notes. *Neurotexis termon* is very close to *N. maura* (q.v. for discussion) and its allies. As in other species

of this complex, the details of the surstylus offer the most decisive specific characters. There is a possibility that the female specimens listed above include some specimens of *N. despiciens*, as I have no information as to how they may be distinguished.

Etymology. The specific epithet is from the Greek noun *termon*, a limit or end, in reference to the terminal modification of the surstylus.

Neurotexis kaplanae n.sp.

Fig.3

Material examined. HOLOTYPE male, Madagascar: Tsimbazaza, Antananarivo (Tananarive), 14 Apr. 1991, A.F. & F.K. (USNM). PARATYPES, 5 males, same data (AM, TAU, USNM); 1 male, Mandraka, 75 km east of Antananarivo, 16 Apr. 1991, A.F. & F.K. (TAU). Other material (not types): 11 females, same data as holotype (AM, TAU, USNM); 1 female, Mandraka, 16 Apr. 1991, A.F. & F.K. (TAU).

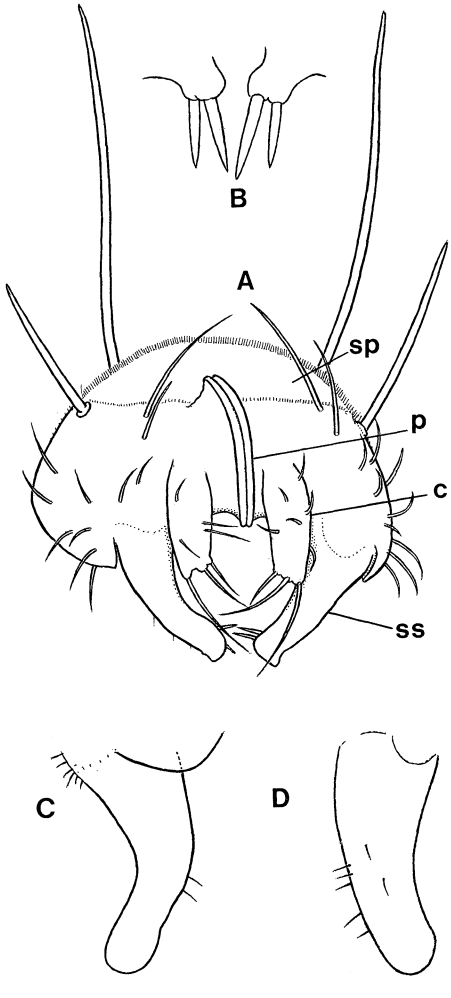

Fig.4. *Neurotexis termon*. A, epandrium and associated structures, posterior aspect; B, gonites, posterior aspect; C, right surstylus, outer aspect. *Neurotexis delphis*. D, left surstylus, outer aspect. c – cercus; p – proctiger; sp – silvery pruinescent zone on epandrium; ss – surstylus.

Description. Very similar to *N. maura*, agreeing with description of that species except as indicated below.

Colouration. Cephalic bristles predominantly dark brown to blackish; cheek bristles usually yellow, sometimes darker. Terminal segment of mid and hind tarsi yellowish, not noticeably darker than preceding segments. Abdominal tergite 2 yellowish on almost anterior half.

Thorax. Hind femur in male with series of ventral bristles occupying short zone before basal third of length of femur. Costal index 2.4-2.9; vein 4 index 5.7-8.0.

Abdomen. Male postabdomen: tergite 6 broad, lateral margin with about 4 bristles, of which at least one other is much more than half as long as posterior one; surstylus moderately elongate, slightly recurved, a little incurved at base only, with apex rounded, convex on outer surface, planate on inner surface, with 2 or 3 thick bristles, often asymmetrically arranged, on distal part of inner surface near posterior side; gonite with 2 large bristles and a small setula; distiphallus with a series of long denticles, each about 4.0 μm long, along right side of sub-basal part.

Dimensions. Total length, male 2.3-2.7 mm, female 2.0-2.5 mm; length of thorax, male 0.7-1.0 mm, female 0.8-1.0 mm; length of wing, male 1.6-2.2 mm, female 1.6-2.0mm.

Distribution. Madagascar – central and central-eastern districts.

Notes. *Neurotexis kaplanae* belongs in the difficult complex of similarly coloured species including *N. maura* (q.v. for discussion). *Neurotexis kaplanae* appears to be generally distinguishable from other species of this complex in the more extensively yellowish anterior zone on abdominal tergite 2, and the paler terminal segment of the mid and hind tarsi. Otherwise determination depends on male postabdominal structures, particularly the stronger bristling of tergite 6, the longer denticles on the distiphallus, and details of the surstylus.

Etymology. The specific epithet refers to the collector, Mrs Fini Kaplan.

Neurotexis delphis n.sp.

Fig.4

Material examined. HOLOTYPE male, Madagascar: Emoty, near Fort Dauphin (Taolanaro), 19 May 1987, D.K.M. (AM). PARATYPES, 9 males, 18 females, same data (AM, BM, NAT, USNM); 6 males, 25 females, south of Mahatalaky, Fort Dauphin district, 18 May 1987, D.K.M. (AM, CNC, MNM); 1 male, 5 km west of Fort Dauphin, 21 Apr. 1991, A.F. & F.K. (TAU); 2 males, 3 females, Fort Dauphin, 18-23 Apr. 1991, A.F. & F.K. (TAU); 1 female, Ranomafana, 800 m, 27 Apr. 1991, A.F. & F.K. (TAU).

Description. Resembling *N. maura*, agreeing with description of that species except as indicated below.

Colouration. Postfrons with bristles brown to blackish; cheek bristles yellow or brownish yellow; major bristles of antennal segment 2 black. Mesoscutum and scutellum black to brown-black with largely dark pruinescence and blackish bristles, ground colour of mesoscutum with pair of yellowish tawny zones posteriorly of very variable extent but each zone usually enclosing both dorsocentral bristles of that side, sometimes zones fused medially; a large zone of pale grey pruinescence covering central and posterior part of mesoscutum, as in *N. maura*, somewhat obscuring yellowish tawny zones; mesopleuron largely dark brown; sternopleuron yellow. Hind femur blackish on slightly less than distal half; terminal segment of mid and hind tarsus variably browned. Wing membrane tinged with brown at apex; alula brown. Abdominal tergite 2 broadly pale yellowish on anterior part; tergites 3 to 6 with variable pale yellowish anterior zones, often absent in male; abdominal sternites predominantly pale yellowish in female, posterior ones variably browned in male. Hind femur of male with about 4 ventral bristles on basal third of its length only; hind tibia of male with well developed almost straight acute apical posteroventral tooth. Costal index 2.6-3.2; vein 4 index 4.8-6.5.

Abdomen. Male postabdomen: surstylus elongate, slightly curved in a posterior direction, slightly broadened basally, tapered for much of length, with rounded apex, with one or few weak bristles on inner surface near apex, much smaller than in *N. termon, N. kaplanae*, and allied species, little larger than sparse setulae elsewhere on surstylus; each hypandrial plate with 2 closely placed unequal bristles, outer one much more slender; gonite broad basally, narrowed distally (in posterior aspect), with 2 thick terminal bristles; aedeagus with a series of sparse, finely pointed sub-basal denticles on right side, each about 2.4 μm long.

Dimensions. Total length, male 2.1-2.5 mm, female 1.8-2.6 mm; length of thorax, male 0.9-1.0 mm, female 0.8-1.1 mm; length of wing, male 1.9-2.1 mm, female 1.6-2.3 mm.

Distribution. Madagascar – southern and south-eastern districts.

Notes. *Neurotexis delphis* is similar to *N. maura* and its allies (*N. despiciens, N. termon*, and *N. kaplanae*) but is paler, particularly in the entirely yellowish sternopleuron and partly pale ground colour of the mesoscutum. The surstylus of *N. delphis*, with one short bristle, has the bristling less developed than in those species.

For discussion of its relationship to *N. stuckenbergi*, see under that species.

Etymology. The specific epithet is the Greek form of the French *dauphin* (dolphin or French crown prince) in reference to the locality Fort Dauphin, in the vicinity of which the species is common.

Neurotexis stuckenbergi (McAlpine) n.comb.

Neurochaeta stuckenbergi McAlpine, 1978: 283-284, figs 5-8, 12.

Material examined. HOLOTYPE female, Madagascar: Fénérive, Dec. 1955, B.R.S. (PM) - re-examined Sept. 1990.

Distribution. Madagascar – central-east.

Notes. The original description covers most significant features of the type specimen. The venation in my figure 8 (McAlpine, 1978) is slightly distorted because of curvature of the wing, the discal crossvein being more than half as long as the distal section of vein 4. Also the head is not as short as in my Figure 6.

Neurotexis stuckenbergi is still only known with certainty from a single female. It seems very close to *N. delphis* and may be conspecific. In view of the often small differences between species, sometimes not apparent in females, the fact that none of the long series of *N. delphis* has pale major bristles on antennal segment 2 as in the type of *N. stuckenbergi*, and the lack of information on the host plant of the latter species, I provisionally regard these as separate species. The type of *N. stuckenbergi* is somewhat faded, but was less so when I drew up my description in 1977. I do not think fading accounts adequately for the difference in bristle colouration.

Neurotexis charis n.sp.

Fig.5

Material examined. HOLOTYPE male, Madagascar: vicinity of Emoty, Fort Dauphin (Taolanaro) district, 19 May 1987, D.K.M. (AM). PARATYPES, 1 male, 2 females, south of Mahatalaky, Fort Dauphin district, 18-19 May 1987, D.K.M. (AM); 1 male, north of Fort Dauphin, 20 May 1987, D.K.M. (AM); 18 males, 32 females, Fort Dauphin, 18-23 Apr. 1991, A.F. & F.K. (AM, BM, TAU, USNM); 9 males, 6 females, 5 km west of Fort Dauphin, 21 Apr. 1991, A.F. & F.K. (TAU, USNM). Other material (not types): 1 female, An'obo, 190 m, Forêt Antsingy, Antsingy, Antsalova district, about 18°45'S 44°50'E, Sept. 1957, P. Griveaud (NAT); 5 males, Tsimbazaza, Antananarivo, 14 Apr. 1991, A.F. & F.K. (AM, TAU, USNM); 1 male, 2 females, Andasibe (Perinet), 16-17 Apr. 1991, A.F. & F.K. (TAU); 3 males, 6 females, Ranomafana, 800 m, 27 Apr. 1991, A.F. & F.K. (AM, TAU).

Description. *Colouration.* Head and its appendages pale yellowish; occiput largely brown; inner and outer vertical, ocellar, fronto-orbital, and postgenal bristles, and dorsal bristles on antennal segment 2 brown to black, other cephalic bristles pale yellowish. Thorax brown-black with black to brown bristles and setulae, those setulae on sternopleuron yellow; mesoscutum with large yellow zone extending from scutellar suture to in front of centre and laterally to postalar bristle; humeral callus tawny; scutellum with yellow apex; subscutellum with

large, shining, silvery-white pruinescent central zone, brown laterally. Legs yellow; distal quarter of hind femur blackish. Wing hyaline, with yellowish veins; alula greyish. Haltere pale yellowish. Abdominal tergites 3-7 and posterior part of tergite 2 brown, remainder of tergites pale yellowish; ventral surface of abdomen pale yellowish, with lateral margins brown, more broadly so posteriorly and more extensively so in male than in female; epandrium with large silvery-white pruinescent zone.

Head higher than long; postfrons, near middle, nearly half as wide as head; face, on lower part, broadly convex, receding toward epistomal margin; fronto-orbital bristles moderately long and strong, the inclinate one inserted slightly behind level of anterior reclinate one, incurved but not at all reclinate; inner vertical bristle shorter than fronto-orbitals; postvertical bristles parallel; vibrissa succeeded by 3 or 4 cheek bristles of similar size. Antenna: segment 6 of arista with dorsal rays 5 or 6 on basal part, 3 distally with gap beyond first, ventral rays 3 or 4, all distal, medial rays 2-4, all distal, and with short terminal fork.

Thorax rather short and robust, dorsally convex; 2 unequal dorsocentral bristles present, posterior one conspicuously longer than scutellum, anterior one at least as long as its distance from posterior one; presutural bristle distinct; prescutellar acrostichal bristle absent; only 1 distinct supra-alar bristle (as distinct from postalar) present; major scutellar bristle much longer than scutellum; a long posterior sternopleural bristle present, with somewhat shorter bristle close in front of it, but sternopleuron without anterior bristles or special group of setulae. Legs of moderate dimensions; mid coxae approximated but not contiguous; femora increasing in length in the order fore, mid, hind; fore femur with 5-7 dorsal bristles, about 5 large posteroventral and no anteroventral bristles; mid femur with a series of up to 7 short anterior to anteroventral bristles; hind femur with a large anterior bristle at about apical fifth, 1 large dorsal bristle at about same level, 1 or 2 smaller dorsal bristles further basad, and some weakly differentiated ventral bristles near base; mid tibia with about 5 short, thick black apical anterior setulae, and a large straight apical ventral spur; hind tibia with 2 small but well differentiated apical anteroventral spurs. Costa produced at subcostal break into an elongate lappet which is shorter than that of *N. stuckenbergi* and *N. polyaster*; anal cell narrow; anal crossvein strongly bent; vein 6 somewhat sclerotised; costal index 2.2-2.4; vein 4 index 4.2-5.3.

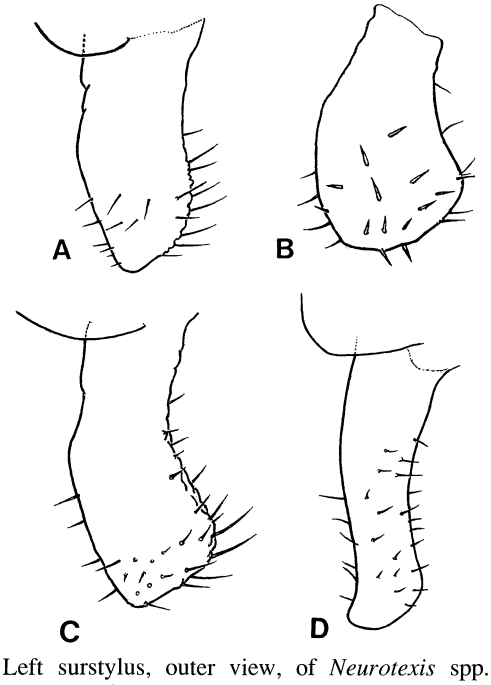

Fig.5. Left surstylus, outer view, of *Neurotexis* spp. A, *N. charis*, holotype; B, *N. charis*, near Mahatalaky, detached; C, *N. charis*, Fort Dauphin; D, *N. primula*.

Abdomen broad. Male postabdomen somewhat similar to that of *N. maura*; surstylus very variable in shape, typically about 2.4 times as long as broad in outer aspect, parallel-sided or variably expanded distally, a little curved in posterior direction, often subangular anteriorly at the slightly outwardly curved apex, sometimes much broadened distally or obovate-spatulate, setulose in part but without strong bristles, its surface with very variable, often reticulate rugosity; each hypandrial plate with 2 long bristles; gonite more elongate than in *N. maura*, with 3 long, more or less unequal bristles.

Dimensions. Total length, male 1.5-2.1 mm, female 1.6-2.4 mm; length of thorax, male 0.6-0.8 mm, female 0.6-0.9 mm; length of wing, male 1.4-1.8 mm, female 1.5-1.9 mm.

Distribution. Madagascar - widely distributed.

Notes. *Neurotexis charis* is apparently a remarkably variable species, though the essential characters given in the key are constant in the available series of 76 examples. Specimens from Ranomafana, Andasibe, and one from Tsimbazaza have the mid femora largely blackish and hind femora more extensively so than in other specimens, but male genitalia characters match those of typical specimens with paler femora. The shape of the surstylus is surprisingly variable, but apparently shows no group consistency which could be used to distinguish closely related species, nor does the variation fit a geographic pattern. This is in sharp contrast to the group of very similar species including *N. maura, N. kaplanae, N. termon* and *N. despiciens*, where differences in the surstylus are evidently specific.

Etymology. The specific epithet is from the Greek *charis*, grace or beauty.

Neurotexis primula n.sp.

Figs 1, 5

Material examined. HOLOTYPE male, Madagascar: Emoty, near Fort Dauphin (Taolanaro), 19 May 1987, D.K.M. (AM).

PARATYPES, 2 males, 8 females, same data (AM); 6 males, 23 females, south of Mahatalaky, Fort Dauphin district, 18 May 1987 (AM, BM, NAT); 8 male, 36 female, Fort Dauphin, 18-23 Apr. 1991, A.F. & F.K. (TAU, USNM); 1 male, 1 female, 5 km west of Fort Dauphin, 21 Apr. 1991, A.F. & F.K. (TAU).

Description. *Colouration.* Head creamy white; postfrons pale yellow; bristles on postfrons yellowish brown, those on cheek yellow, those on antennal segment 2 yellowish brown to dark brown. Antenna pale yellow. Proboscis and palpus deeper yellow, slightly paler ventrally, with dorsal bristles and hairs dark brown, other bristles and hairs paler; mesoscutum with short, broad dark brown zone, largely concealed by head, at anterior extremity; scutellum dark brown with large orange apical zone; subscutellum dark brown laterally, with large, shining silvery-pubescent central zone. Legs yellow, about apical fifth of hind femur brown-black. Wing hyaline, with yellowish veins. Haltere pale yellowish. Abdominal tergite 1 and much of tergite 2 yellow, remainder of tergites yellowish to brown (very variable in the dried material, females often paler); in male, epandrium with large silvery-pubescent zone; ventral surface of abdomen yellowish, with variable brown suffusion.

Head of somewhat similar proportions to that of *N. charis* and *N. stuckenbergi*; fronto-orbital bristles slightly longer than in the above species; inclinate fronto-orbital strongly incurved, not at all reclinate, inserted well behind level of anterior reclinate bristle; postvertical bristles parallel, thicker than in other species. Antenna as described for *N. charis*.

Thorax similar to that of *N. charis*, less depressed than in *N. maura, N. delphis*, and allied species; only the long posterior dorsocentral bristle present; 2 unequal posterior sternopleural bristles present. Legs similar to those of *N. charis*; hind femur with a series of short, strong, dark ventral bristles near and before middle in male, much reduced and pale in female. Costal lappet similar to that of *N. charis*; costal index 2.4-2.8; vein 4 index 3.5-5.3.

Abdomen. Male postabdomen generally as described for *N. delphis*; surstylus elongate, slightly compressed at the rounded apex, not broadened basally, with numerous short setulae; each hypandrial plate with 2 widely spaced bristles, outer one particularly long; gonite somewhat elongate, with 2 apical bristles and a small anterior setula, and a rounded anterior projection at base.

Dimensions. Total length, male 1.9-2.4 mm, female 2.0-2.6 mm; length of thorax, male 0.8-0.9 mm, female 0.9 mm; length of wing, male 1.7-2.0 mm, female 1.8-1.9 mm.

Distribution. Madagascar – south east.

Notes. *Neurotexis primula* differs from other species of the *stuckenbergi* group in having a single pair of dorsocentral bristles and the yellow thorax with very little darker colouration. In the field the yellow colour with conspicuous brown eyes (when viewed with a magnifying loupe) helps identification. *Neurotexis vesca* has somewhat similar colouration, but the thorax is much depressed.

Etymology. The specific epithet is from the Latin noun *primula*, a primrose, in reference to the colouration.

Neurotexis vesca n.sp.

Fig.6

Material examined. HOLOTYPE female (unique), Madagascar: south of Mahatalaky, Fort Dauphin (Taolanaro) district, 18 May 1987, D.K.M. (AM).

Description of female (male unknown). *Colouration.* Yellow dorsally, creamy-white ventrally; bristles and hairs pale yellowish; specialised silvery pruinescence absent from all parts. Antenna, legs, and haltere pale yellowish. Wing clear, with yellow veins; costal bristles and spinules brown.

Head slightly depressed, height about 0.8 of length; width of postfrons near middle 0.53 width of head, its length slightly less than width; fronto-orbital plate most strongly sclerotised along eye margin, not demarcated on medial side from the apparently broad mesofrons, extensively setulose, but with single almost regular series with posteriorly curved apices close to eye margin; fronto-orbital bristles quite short (middle reclinate one differing much in position between right and left sides of holotype); postvertical bristles strongly divergent; cheek bristles as in *N. polyaster*; eye narrowly oblique. Antenna with ventral bristle on segment 2 fine, not reaching beyond centre of face.

Thorax moderately depressed, broadest across the prominent, tumid humeral calli; postnotal structures not as deep as in *N. primula* and related species, less dorsoventrally compressed than in *N. polyaster*; chaetotaxy similar to that of *N. polyaster*; anterior sternopleurals absent. Legs relatively longer than in *N. polyaster*, more slender than in all other *Neurotexis* spp.; fore femur with dorsal bristles less strongly differentiated than in *N. polyaster*, with 3 or 4 posteroventral bristles; mid femur with poorly differentiated anterior bristles; hind femur tapered and slightly curved basally, with one anterior bristle at about apical quarter and 3 dorsal to anterodorsal bristles, one near middle of length and 2 more distally placed; mid tibia with armature slightly weaker than that of *N. charis*; hind tibia with one weakly differentiated apical anteroventral bristle. Costa with very short lappet at subcostal break, surmounted by rather short terminal bristle; anal cell narrow; anal crossvein indistinct; costal index 3.3; vein 4 index 5.5.

Abdomen moderately broad, only sternites 4 and 5 as broad as tergite of respective segments, only sternites 5 and 6 with distinct bristle at each posterolateral angle;

cercus tapering near base, slender for much of length, with several moderately long setulae.

Dimensions. Total length 2.2 mm; length of thorax about 0.9 mm; length of wing 2.0 mm.

Distribution. Madagascar – south-east.

Notes. *Neurotexis vesca* is apparently related to *N. freidbergi* and *N. polyaster* because of the two supra-alar bristles, scarcely convex face, and depressed form. It is distinguished from all other species of *Neurotexis* by the vestigial costal lappet, absence of shining silvery pruinescence on the subscutellum and elsewhere, and entirely pale yellowish thorax.

Etymology. The specific epithet is a Latin adjective, wasted or thin, in reference to the small size and slender body and legs.

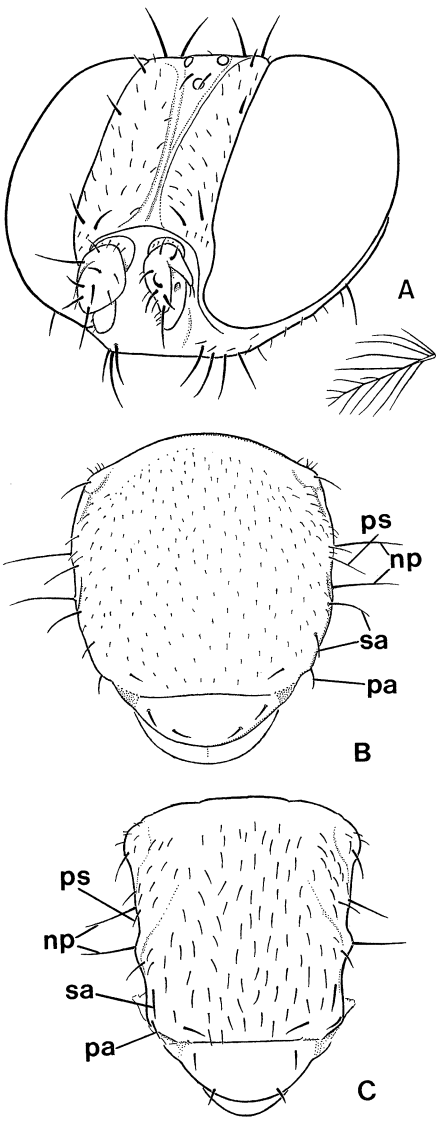

Fig.6. *Neurotexis polyaster.* A, head, left arista (segment 6) shown separately; B, thorax, dorsal aspect. *N. vesca.* C, thorax, dorsal aspect. np – notopleural bristles; pa – postalar bristle; ps – presutural bristle; sa – supra-alar bristles.

Neurotexis freidbergi n.sp.

Fig.8

Material examined. HOLOTYPE male, Madagascar: Fort Dauphin (Taolanaro), 18-23 Apr. 1991, A.F. & F.K. (USNM). PARATYPES, 10 females, same data (TAU, USNM, AM).

Description. Characters as given for *N. polyaster*, except as indicated.

Colouration. Fronto-orbital plate grey-black, with silvery pruinescence; interfrontal tawny, with greyish white pruinescence; face, parafacial, and anterior part of cheek greyish brown; postvertical and all strong cheek bristles black. Antenna yellowish grey, with segment 2 partly darker. Labella tawny to brownish. Mesoscutum with shining pruinescence abruptly bicoloured, largely yellowish with narrow silvery lateral zones demarcated by dorsocentral lines. Hind femur yellowish at base, scarcely yellowish at apex; fore tibia with large blackish brown zone not reaching extremities. Abdominal tergites with desclerotised spots arranged as in *N. polyaster*, but broader and, in female, less brilliantly shining in posterior aspect, in male absent from tergite 6; epandrium of male with silvery pruinescent posterior zone; abdominal sternites yellowish brown to dark brown.

Head not depressed, higher than long; postfrons near middle 0.31-0.32 as wide as head, 1.6-1.7 times as long as wide, markedly narrowing posteriorly; fronto-orbital plate slightly variable, anteriorly usually markedly broader than interfrontal; interfrontal concave anteriorly but without linear groove, broader than in *N. polyaster*; fronto-orbital bristles, particularly the 2 anterior pairs, larger than in *N. polyaster*; inner vertical bristles larger than in *N. polyaster*, more closely placed and usually crossed near apices; usually 5 large and one or 2 smaller cheek bristles behind vibrissa. Antennal segment 2 with one well differentiated but not large ventral bristle; arista with about 9 dorsal rays (not including terminal fork and shorter medial rays).

Thorax of similar form to that of *N. polyaster* but only moderately depressed and slightly less broad; most thoracic bristles longer than in *N. polyaster*; major scutellar bristles longer than scutellum, less widely separated than in other *Neurotexis* species. Fore femur with about 7-11 dorsal to posterodorsal bristles. Wing broader than in other *Neurotexis* species; costal index 2.3-2.6; vein 4 index 5.2-6.9.

Abdomen. In male only sternites 4 and 5, in female sternites 4 to 7 as broad as tergites; male sternite 5 with a series of posterior marginal bristles, least developed medially. Male postabdomen as described for *N. stuckenbergi* except as indicated; surstylus broad, not much tapered, slightly curved, very obtuse. Each paired hypandrial plate with 2 short, stout bristles; gonite somewhat elongate, terminating in 2 divergent spine-like bristles. Spines of basiphallus long and curved. Cercus slightly compressed and subtruncate at ventral end.

Dimensions. Total length, male 4.1 mm, female 3.7-4.1 mm; length of thorax, male 1.4 mm, female 1.4 mm;

length of wing, male 2.9 mm, female 2.6-2.9 mm.

Distribution. Madagascar – south-east.

Notes. *Neurotexis freidbergi*, the largest species of *Neurotexis*, is closely related to *N. polyaster*, but is distinguished by the characters given in the key. It also has more numerous cheek bristles and more dorsal rays on the basal part of antennal segment 6 than in *N. polyaster*.

Etymology. The specific epithet refers to the collector, Dr Amnon Freidberg.

Neurotexis polyaster n.sp.

Figs 6, 7

Material examined. HOLOTYPE female, Madagascar: south of Mahatalaky, Fort Dauphin (Taolanaro) district, 19 May 1987, D.K.M. (AM). PARATYPES, 1 female, Fort Dauphin, 18-23 Apr. 1991, A.F. & F.K. (USNM); 1 female 5 km west of Fort Dauphin, 21 Apr. 1991, A.F. & F.K. (TAU).

Description of female (male unknown). *Colouration.* Fronto-orbital plate brownish densely covered with shining silvery pruinescence; remainder of postfrons dark greyish, dull-pruinescent, interfrontal yellowish at anterior extremity only; face, parafacial, and anterior part of cheek dull yellowish; postgena grey-pruinescent, darker posteriorly, the pruinescence somewhat silvery from certain angles; occiput dull blackish; cephalic bristles, except postvertical and some cheek bristles, black; frontal setulae yellowish. Antenna dull yellowish, with slight brown suffusion; dorsal bristles on segment 2 black. Palpus brown, with pale setulae; proboscis brown with yellowish labella. Thorax with dark brown to blackish ground colour; mesoscutum, except on lateral margin in front of transverse suture, thickly ashy-grey pruinescent, the pruinescence appearing silvery in posterior aspect; pleura largely with dark grey to brown pruinescence; zone on upper part of mesopleuron with lighter grey pruinescence, silvery in posterior aspect; thoracic bristles mostly black. Coxae brown; femora brown-black, narrowly yellowish apically; fore femur yellowish brown ventrally; mid and hind femora yellowish basally; fore tibia tawny-yellow; mid and hind tibiae brown-black, narrowly yellowish basally. Wing clear, with yellowish veins. Haltere tawny, with white capitellum. Abdominal tergites blackish brown; tergite 1 largely brown; tergites 2-6 with transverse, silvery pruinescent, desclerotised spot at each posterolateral angle (spots appearing dull greyish tawny in anterior aspect); epiproct silvery pruinescent; sternites 1 to 6 brown to yellowish brown, usually becoming dark brown laterally.

Head obliquely depressed; postfrons near middle 0.38 as wide as head, about 1.4 times as long as wide; fronto-

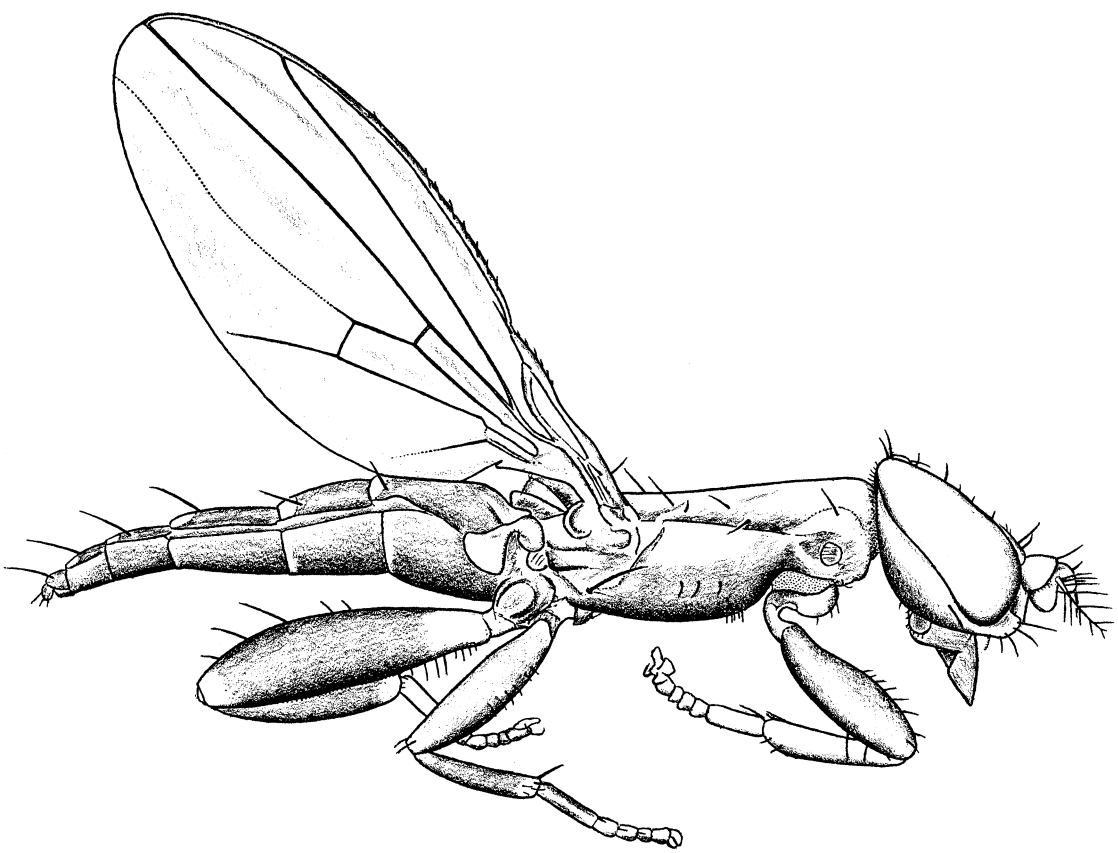

Fig.7. *Neurotexis polyaster* - holotype.

orbital plates very broad, anteriorly very narrowly separated; interfrontal anteriorly with linear median groove; fronto-orbital bristles short but rather stout; postvertical bristles parallel or slightly convergent; 4 cheek bristles behind vibrissa, posterior one or 2 weaker. Antenna similar to that of *N. charis*, but ventral bristle on segment 2 little differentiated from adjacent setulae; arista with 5 or 6 dorsal rays.

Thorax very strongly depressed, broad, but slightly narrowed anteriorly; scutellum and postnotal parts strongly dorsoventrally compressed but structurally similar to those of other *Neurotexis* spp.; chaetotaxy as given for *N. charis* except as follows; dorsocentrals one short pair only; supra-alars 2, posterior one located more dorsally, but not to be interpreted as an intra-alar on account of its longitudinal alignment with postalar; both scutellars shorter than scutellum, major one suberect; posterior sternopleural bristle single, much inclined forwards as in Coelopidae; 3-5 shorter upper anterior sternopleurals, and a tuft of lower anterior sternopleural setulae present; metasternum widely exposed. Legs rather short, hind leg least so; fore coxae not widely separated; mid coxae very widely separated; femora stout, fore and mid ones subequal in length, hind femur longer; fore femur with about 7 dorsal to posterodorsal bristles and 4 or 5 posteroventral bristles; mid femur with about 4 short anteroventral bristles near middle; hind femur with 1 anterior bristle at about apical quarter and a series of about 3 dorsal bristles distally, ventrally near base with fine erect setulae only; mid and hind tibiae as in *N. charis*. Wing as described for *N. charis*; costal index 2.9-3.2; vein 4 index 5.0-6.1.

Abdomen very broad; sternites broad; sternites 4 to 7 as broad as tergites, bristled posterolaterally; cercus short and broad, with one black bristle and minute setulae.

Dimensions. Total length 3.2-3.3 mm; length of thorax 1.2 mm; length of wing 2.3-2.6 mm.

Distribution. Madagascar – south-east.

Notes. *Neurotexis polyaster* is closely related to *N. freidbergi*, but differs in the characters given in the key. The thorax is more strongly depressed than in any other species of *Neurotexis*. In this character it resembles *Neurochaeta magnifica* McAlpine of Papua New Guinea, but, apart from the generic characters, it differs from that species in having the fore coxae relatively close together and the prosternum very narrow.

Etymology. The specific epithet is derived from the Greek *polys*, many, and *aster*, a star, in reference to the shining silvery spots on the abdomen.

Morphology of the Antenna

The antenna of cyclorrhaphous Diptera is primarily a six-segmented appendage, a fact that has often been overlooked. Those asserting the four-segmented nature of the antenna regard the distal part or arista as a single segment, whereas in quite numerous unreduced forms the arista (or stylus) clearly consists of three segments separated by distinct intersegmental membranes. This is quite distinct from the "annulate" condition of the flagellum or parts thereof, in many orthorrhaphous Diptera. As each of the segments generally differs structurally from the others, I prefer to extend the terminology of sequential numbering to cover all six segments, rather than to adopt a special name for each. Segments 4 to 6 are conveniently referred to as the arista, because the articulations between these segments are often difficult to discern in whole dried insects.

With the availability of new material of *Neurocytta* and *Neurotexis*, some aspects of evolution of antennal structure in the Neurochaetidae have become clearer. Groundplan conditions for the family have been determined from the morphology of *Anthoclusia* (so far as it is known in this approximate stem group, Hennig, 1965) and *Neurocytta*, with such periscelidids as *Cyamops* Melander and *Scutops* Coquillett as representatives of a related outgroup (see McAlpine, 1983).

Groundplan characters of the neurochaetid antenna. Segment 2 (pedicel) with distal face hollowed, so that much of distal margin is produced into a lamina; with distal margin deeply slit dorsally, dividing marginal lamina into an inner and outer lobe, these lobes diminishing in width and imperfectly separated ventrally; inner lobe with several thick, spinescent bristles; outer lobe with marginal setulae in a regular, comb-like series; distal margin ventrally without differentiated long bristle. Segment 3 (postpedicel, first flagellomere) ovoid, directed downwards at an angle to longitudinal axis of segments 1 and 2, with thick dorsal basal process fitting into hollow of segment 2; with one sensory pit on outer surface; with group of enlarged microtrichia on apical part. Arista consisting of three sclerotised segments (segments 4-6). Segments 4 and 5 microtrichose, approximately symmetrical, 4 very short, 5 compact but longer than 4. Segment 6 long, consisting of main axis which is slightly symmetrically thickened and irregularly microtrichose basally, distally slender with 2 main series (dorsal and ventral) of hair-like rays.

Neurocytta prisca (Fig.8A) departs from the apparent groundplan in the reduction in number of marginal setulae on the outer lobe of segment 2. It is more primitive than other extant neurochaetids in having segment 2 smaller in relation to segment 3, with less developed lobes and without the long ventral bristle present in *Neurotexis* and *Neurochaeta*, and in the less reduced segment 5. It is uncertain if the shortness of the rays on segment 6 and their absence from its microtrichose basal part constitute a plesiomorphy. What is recorded of antennal structure in the fossil *Anthoclusia* spp. (Hennig, 1965, 1969) is inadequate to resolve the question. If *Neurocytta prisca* is plesiomorphic in this

respect, then there must be convergence in the characters of segment 6 between the *Cyamops* lineage and the more advanced neurochaetids. Convergence here is not improbable in view of some similar features in the arista in such diverse flies as *Nothybus* (Nothybidae) and *Glossina* (Glossinidae).

In *Neurotexis* (Fig.8B,C) segment 2 has enlarged lobes with elaborated armature and a long ventral bristle (probably secondarily reduced in *N. vesca*). Segment 3 has the enlarged apical microtrichia relatively long and, at least in some species (*N. freidbergi* and *N. primula*), minutely branched. Segments 4 and 5 are very small, though freely articulated. Segment 6 has the microtrichose basal part strongly swollen, particularly on the dorsal side (as in *Nothybus*), and has very long dorsal and ventral rays, of which three to six dorsal ones are located on the basal swelling, the first of them at the extreme base of the segment (as in *Cyamops*).

The antenna of *Neurochaeta* has most of these features of *Neurotexis*, except that segment 5 is less reduced, and the branching of the apical microtrichia of segment 3 is apparently absent. Thus antennal morphology supports the idea of monophyly for the group *Neurotexis* plus *Neurochaeta* (Woodley, 1982; McAlpine, 1985a).

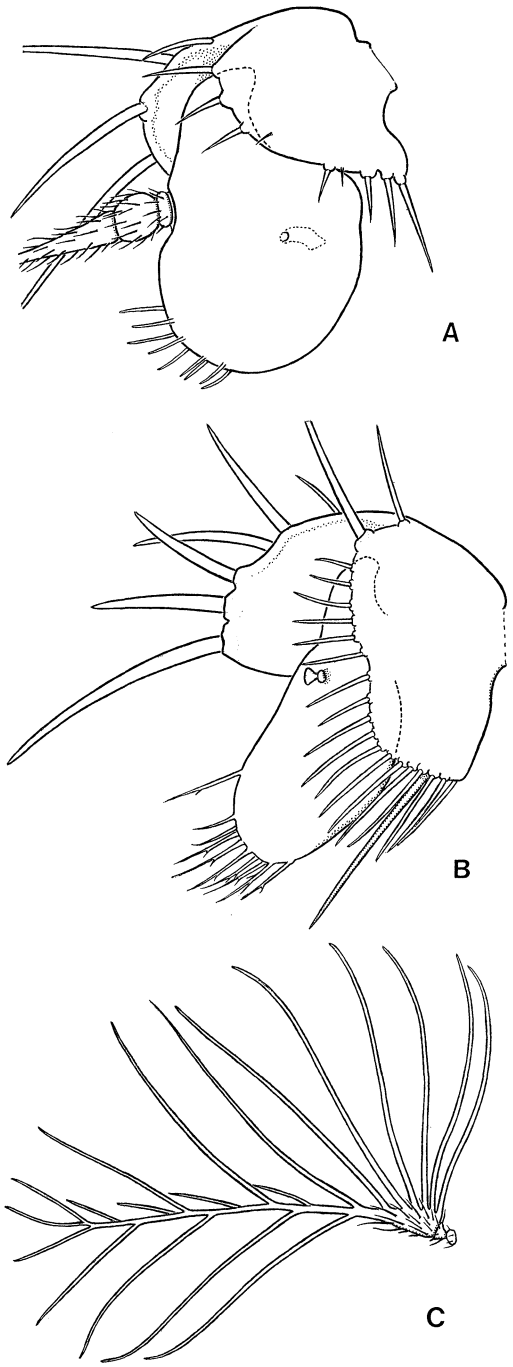

Fig.8. Antennal structures. *Neurocytta prisca*. A, left antenna, segment 1 and part of segment 6 omitted. *Neurotexis freidbergi*. B, left antenna, segments 1 and 6 omitted; C, arista (antennal segments 4-6) at same scale as B.

Field Observations

At 'Banana Grove', Chimanimani National Park, altitude about 1500 m, I found four female adults of *Neurocytta prisca* on suckers (short lateral shoots) less than 1 m high at bases of tall, mature plants of *Strelitzia augusta* Thunberg (family Strelitziaceae, formerly included in Musaceae). These flies could have been fairly numerous in the vicinity, but the leafy crowns of the host plants were out of reach, and access to plants with suckers in the rough terrain was limited by the available time. All plants had single trunks, the suckers apparently not continuing to develop while the main trunk survives. Recruitment rate must be very low, as only three young plants (apparently seedlings) were seen. The plants are of restricted occurrence in the National Park, though numerous at 'Banana Grove'.

The adults of *N. prisca* were seen on leaf blades of *Strelitzia* and one on a petiole, all resting head downwards. They took flight when disturbed.

In a glass tube, adults of *N. prisca* moved less rapidly than the familiar *Neurochaeta inversa*, and not in a zig-zag path. The head downwards position was usually maintained while walking on a vertical surface, but, when at rest, flies did not react promptly to the inversion of the tube (in contrast to spp. of *Neurochaeta* s.str., see McAlpine, 1978). They did not have difficulty in moving from a wall to a ceiling situation, as have *Neurochaeta parviceps* and *N. inversa* (McAlpine, 1988b).

Because two of the specimens obtained on the *Strelitzia* plants were newly emerged (being still teneral more than six hours after capture) it is virtually certain that they were on their host plants.

Numerous adults of *Neurotexis* were found on *Pandanus* (family Pandanaceae, undetermined species) with large, but not broad leaves, growing in damaged forest in a very humid, shaded environment at Andasibe, 15 to 16 May 1987. These flies later proved to be a mixture of *N. termon, N. maura* and *N. despiciens*. The flies sheltered within the appressed young leaves in the centre of the plant and ran out when disturbed. They showed similar head-downwards cursorial behaviour to

that of *Neurochaeta inversa* but I judged their movements to be slower. They flew when pressed.

Neurotexis delphis and *N. primula* were found together on *Ravenala madagascariensis* J.F. Gmelin at localities between Fort Dauphin (Taolanaro) and Mahatalaky in south-eastern Madagascar on 18 to 19 May 1987. They were in boggy habitats with *Sphagnum* in otherwise open grassland. The adults of both *Neurotexis* spp. were found in flowers at anthesis. The flowers contained a sugary nectar, attractive to vespids and bees, and also had much powdery pollen. The flies ran or flew out of the flowers when disturbed, often then running on the petioles, particularly on their imbricate bases. Under the rather hot conditions experienced, they were very active, not only running rapidly in the manner of *Neurochaeta inversa*, constantly oriented with the head downwards, but flying readily also, especially individuals of *N. primula*, which showed very frequent aerial escape behaviour. They often settled again within 20 to 40 cm. When observed in a collecting jar, these two *Neurotexis* spp. (and also a single individual of *N. polyaster*) did not run in such definite zig-zag paths as do *Neurochaeta inversa* and *N. parviceps*, but moved more in the manner of inverted *Stenomicra* spp. (see McAlpine, 1978). The single specimen of *Neurotexis vesca* was collected with the above species on flowering *Ravenala* but was not distinguished from the similarly coloured *N. primula* in the field, as it apparently showed similar behaviour.

Neurotexis charis was collected in small numbers together with *N. delphis* and *N. primula* at the above sites on flowering *Ravenala*. On 20 May 1987 I examined a *Ravenala* plant on a hillside a short distance west of Fort Dauphin. When an inflorescence, long past anthesis, was disturbed, several neurochaetids emerged from the bracts. Only one could be captured and proved to be *N. charis*. It exhibited normal (for *Neurotexis*) head-downwards cursorial behaviour.

The numerous specimens of *Neurotexis* obtained by A. Freidberg and F. Kaplan in Madagascar during April 1991 were all taken on *Ravenala madagascariensis* (*in litt.* and label data). These include *Neurotexis kaplanae, N. delphis, N. charis, N. primula, N. freidbergi* and *N. polyaster* (see lists of material examined under these species for localities). They particularly noted the head-downwards cursorial behaviour of these flies.

Discussion of Host Plants

I previously summarised information on neurochaetid host plants in the Australian and Oriental regions (McAlpine, 1988b). These apparent hosts belong in the families Araceae (order Arales), Pandanaceae (order Pandanales), Zingiberaceae and Musaceae (order Zingiberales). The apparent hosts in the Afrotropical Region belong in the families Pandanaceae and Strelitziaceae (order Zingiberales). These latter are inferred to be larval hosts because they are inhabitated by adult flies and offer phytotelmata probably suitable for the larvae. Also, some of the flies were newly eclosed when found, and could not have moved far from their larval habitat.

Because neurochaetids have been rarely sought in the Afrotropical Region, additional host taxa probably remain to be recorded. Likely host genera of Musaceae in the region include *Ensete* and *Musa*, judging from associations with oriental neurochaetids. My colleague D.A. Barraclough has searched for neurochaetids on *Strelitzia* in likely habitats in South Africa (particularly Natal Province), so far without success.

Some recent observations suggest that adult neurochaetids may at times use for shelter plants other than those in which their larvae live. At Palmerston East, Queensland, 25 January 1991, several individuals of *Neurochaeta inversa* McAlpine were seen resting on the large leaves of *Musa* sp. and some were sheltering in the involute young leaves. Other individuals were on their normal host, *Alocasia*, nearby. Hay & Wise (1991) have reidentified Australian mainland populations of *Alocasia* as *A. brisbanensis* (F.M. Bailey) Domin, so this is accepted as the correct name for the host of *Neurochaeta inversa*. This action does not affect the identification for the host of *Neurochaeta macalpinei* Woodley in Sabah and Palawan which is still presumed to be *Alocasia macrorrhizos* (*L*) G. Don. The record of this species from Palawan, Philippines, is due to R. de Keyzer (AM collection).

Apparent hosts are recorded above for all afrotropical neurochaetid species except *Neurotexis stuckenbergi*, but as yet no species has been found on more than one genus of plants. *Ravenala madagascariensis* apparently supports populations of at least seven *Neurotexis* species and five (perhaps 6) species have been found together on the one group of plants near Mahatalaky. The three species I found living together on *Pandanus* at Andasibe are distinct from any found on *Ravenala*. Freidberg and Kaplan collected only on *Ravenala* at this locality and the one specimen of *Neurotexis* they obtained (a female, probably of *N. kaplanae*) is different from any in my much larger sample. These data suggest a high degree of host specificity in *Neurotexis* species.

In Figure 9 I have superimposed the pattern of apparent host plant associations on a phylogeny of neurochaetid species, omitting those relatively few species for which I have no host data.

The phylogeny is that previously worked out (McAlpine, 1988a) expanded to cover additional species. An undescribed species of *Neurochaeta* collected on *Musa* sp. (Zingiberales: Musaceae) in Thailand by R. de Keyzer (AM collection) is referred to as "Thai sp." in Figure 9. As it is extremely similar to *Neurochaeta parviceps* McAlpine and differs mainly in male postabdominal characters, it is placed for present purposes as a sister species of it. A cladistic treatment of the now numerous species of *Neurotexis* is based on the data discussed under that genus. These data leave a few doubtful relationships in the

phylogenetic system. However, for the present purpose of locating changes in host plant taxa, the main relevant points in this clearly monophyletic genus are: (i) the three species forming the *maura* complex (viz. *Neurotexis maura, N. despiciens*, and *N. termon*) are taken as forming a moderately probable monophyletic group, and (ii) it is very improbable that the *maura* complex forms a sister group to a major part of the species of *Neurotexis*. If the *maura* complex is monophyletic, its sister group is probably *N. kaplanae* alone, or perhaps *N. kaplanae* + *N. delphis* + *N. stuckenbergi* (host of the last species unknown).

The pattern of host association shows a predominant preference for plants of the order Zingiberales, which spreads across the three documented fly genera and includes three of the five Old World plant families included in the order (Table 1). Further interesting features of the pattern are: i) *Neurocytta prisca*, which constitutes a relatively plesiomorphic sister group to all or most of the other neurochaetid species, lives on a plant of this order; ii) the species of *Neurotexis*, except for the 3 species of the *maura* complex, probably constituting a monophyletic group of low phylogenetic order, live on plants of this order; iii) three species of *Neurochaeta*, including one which apparently constitutes a relatively plesiomorphic sister group to all other species of the genus, live on plants of this order.

On the basis of the above data, I propose a hypothesis that the plesiotypic host association for extant taxa of Neurochaetidae is that with the Zingiberales, though at present manifested by diverse associations with three known families and four known genera of this order.

The system presented in Figure 9 involves the lowest possible number of host switches, indicated by a circled S, to explain the existing pattern. The association of neurochaetids with the order Pandanales (family Pandanaceae) can be explained by two independent host changes relatively late in neurochaetid history, once in the genus *Neurotexis* in Madagascar, and once in the genus *Neurochaeta* in New Guinea (or a nearby precursory land mass). The association with the order Arales (family Araceae, genus *Alocasia*) is also explicable by two late host changes, each affecting a single known species of *Neurochaeta*, in Australia and Malesia respectively. An equally parsimonious number of host switches in the branch leading to *Neurochaeta inversa* and *N. magnifica* can be obtained by an initial switch, before the furcation of this branch, from Zingiberales to Arales, followed by a switch of one sister species to Pandanales, or vice versa. My only reasons for preferring the system shown in Figure 9 are the weakness of the shared synapomorphies of *N. inversa* and *N. magnifica* and the great degree of morphological divergence between them.

Alternatively, the most parsimonious explanation for the pattern of present host associations may not be the

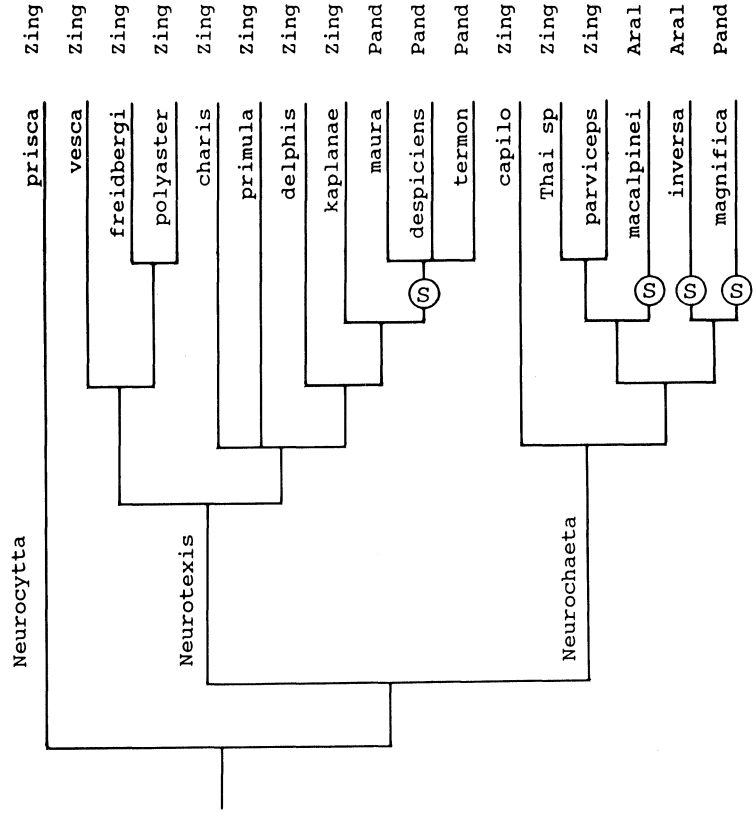

Fig.9. Cladogram of species of Neurochaetidae, showing orders of host plants, fly species with unknown hosts omitted. S – possible points of switch of host order from hypothetical plesiotypic zingiberalean association. Aral – Arales; Pand – Pandanales; Zing – Zingiberales.

historically correct one. There is a possibility of any lineage surviving a temporary loss of access to a zingiberalean host, if it has an accessible alternative host. In view of direct evidence of a number of host switches, the suitability of a number of both zingiberalean and other monocot taxa as neurochaetid hosts, and the long, largely undocumented neurochaetid evolutionary paths, such a host sequence as Zingiberales sp. a —> other monocot sp. —> Zingiberales sp. b is not highly improbable.

The group of zingiberalean families, including Musaceae, Strelitziaceae and Heliconiaceae, was considered as a single family, Musaceae s.l., in older literature (eg, Willis, 1951), and the first two of its components provide host plants for more than half the host-known species of Neurochaetidae. A representative of this plant group is utilised by *Neurocytta prisca*, the recent species which is closest morphologically to the Eocene-Oligocene *Anthoclusia* of northern Europe. The genus *Musophyllum*, which occurred in the arctic in the late Paleocene to early Eocene (Boyd, 1990), is apparently referable to Musaceae s.l., and in the early Tertiary the Nearctic and Palearctic biotas were not very distinct. It is inferred that such zingiberalean plants or related forms may well have been accessible to *Anthoclusia* and may conceivably have been utilised as hosts.

Table 1. Monocot host taxa and associated neurochaetid species.

Zingiberales – Strelitziaceae
Strelitzia augusta
Neurocytta prisca
Ravenala madagascariensis
Neurotexis vesca
Neurotexis freidbergi
Neurotexis polyaster
Neurotexis charis
Neurotexis primula
Neurotexis delphis
Neurotexis kaplanae

Zingiberales – Musaceae
Musa spp.
Neurochaeta capilo
Neurochaeta sp. (Thailand)

Zingiberales – Zingiberaceae
Zingiber spectabile
Neurochaeta parviceps

Pandanales – Pandanaceae
Pandanus spp.
Neurotexis maura
Neurotexis despiciens
Neurotexis termon
Neurochaeta magnifica

Arales – Araceae
Alocasia brisbanensis
Neurochaeta inversa
Alocasia macrorrhizos
Neurochaeta macalpinei

Thus, the association between neurochaetids and banana-like plants may have continued for about 40 million years.

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