

# Fossil flies in Baltic amber – insights in the diversity of Tertiary Acalyptratae (Diptera, Schizophora), with new morphological characters and a key based on 1,000 collected inclusions

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**Abstract:** A review of specific publications dealing with Baltic amber Diptera, Acalyptratae, from the years 1822 until 2008 includes 38 articles. H. LOEW was the first entomologist searching systematically for Diptera in amber. Two of his three articles are discussed. Parts of his first one (1850) are translated from German because of its extreme rarity in libraries. From Eocene Baltic amber 35 families of acalyptates are known now, a further four from British Eocene sediments. Natalimyzidae, Piophilidae and Pyrgotidae are recorded for the first time, *Natalimyza* was known only from the recent Afrotropical fauna. Different counts of the percentage of acalyptates among insect-, Diptera- and "true fly"-inclusions, respectively, are compared. Less than 1% of all flies belong here. Reasons for this rarity are discussed together with an overview of the rare aggregation of acalyptates in single amber pieces. Peculiar morphological apomorphies, which enable family identification worldwide because of their singularity, were already present during the Tertiary. Three such examples are discussed. The dispute about the doubted synchronous genesis of German Bitterfeld amber is solved by demonstrating 15 conspecific acalyptate species in both deposits. Intraspecific variability of an amber acalyptate has never been studied before. On the basis of 45 specimens and the holotype of *Protoscinella electrica* (Chloropidae) the slowness of evolutionary transformations is exemplified with the background of the phylogenetic value of 16 selected characters. A spotlight is thrown on the polyphyletic reduction process in wing venation and bristle equipment observed in several families of acalyptates.

The systematic part presents overviews of a large number of morphological details used for taxonomy. Two tables enable the easy check and documentation of each detected specimen, as well as an understanding of the puzzling termini and abbreviation systems in subsequent periods of dipterology. Two differently organized identification keys are presented: one listing 97 exceptional, rare, or newly detected morphological peculiarities, a second one is a trial to key out all 56 described and all 161 detected undescribed species. The well known terminology of HENNIG's publication series on amber is used in order to enable an easy cross-reference to his partly complicated descriptions, to his plenty of figures, and to the dipterous literature until the year 1981 when a new terminology was proposed. All family- and generic transfers since HENNIG's times are listed with their references, as well a species breakdown of parts of the identified 1,141 inclusions.

**Key words:** Apomorphies, Bitterfeld amber, Calyptratae, chaetotaxy, Chloropidae, Pyrgotidae, speciation, variability.

**Santrauka:** 1822-2008 metais paskelbtos 38 moksliškės publikacijos, skirtos Baltijos gintare rastiems Diptera, Acalyptratae vabzdžiams. H. LOEWAS buvo pirmasis entomologas, sistematikai tyrinėjės dvisparnius gintare. Aptariami du iš trių jo straipsnių. Atskiros jo pirmojo darbo (1850) dalys yra išverstos iš vokiečių kalbos, nes publikacija yra tapusi didele bibliografine retenybe. Iš eoceninio Baltijos gintaro dabartiniu metu žinomas 35 akalipratinių dvisparnių (Acalyptratae) šeimos. Dar trys rastos eoceninėse nuogulose Didžiojoje Britanijoje. Agromyzidae, Natalimyzidae, Piophilidae, Pyrgotidae ir Sphaeroceridae yra aprašomos pirmą kartą, *Natalimyza* buvo žinoma tik iš dabartinės Afrikos tropikų faunos. Palyginami skirtingu autoriu pateikiami akalipratų gausumo paskaiciavimai tarp visų vabzdžių, dvisparnių ir "tikruju musių" inkliuzų. Šioms musėms priklauso mažiau negu vienas procentas gintare randamų inkliuzų. Šio retumo priežastys aptariamos kartu apžvelgiant retai pasitaikančias akalipratų sankupas viename gintaro gabale. Ypatingos ir kartu unikalios morfologinės apomorfijos, kuriomis pasižymi visos Žemės rutulyje sutinkamos akalipratinių musės, egzistavo jau terciare. Aptariami trys tokie pavyzdžiai. Diskusija apie abejotiną tą pačią vokiškojo Bitterfeldo ir Baltijos gintarų kilmę išsprendžiama parodant, kad abiejuose gintaruose randama 15 vienodų Acalyptratae rūsių. Vidinis rūšinis variavimas tarp gintaruose randamų akalipratų anksčiau nebuvę tirtas. Remiantis 45 pavyzdžiais ir *Protoscinella electrica* (Chloropidae) holotipu demonstruojamas evoliuciinių transformacijų lėtumas kartu pagrindžiant 16 parinktų požymiu filogenetinių reikšmingumą. Nušviečiamas polifiletinis sparno gylslotumo ir šeriutumo redukcijos procesas, stebimas keliose akalipratų šeimose.

**Table 1:** Collocation of aggregated acalyptates in one piece of amber. Each comma separates one stone.

Family	Species	♂♂: ♀♀
Camillidae	<i>Protocamilla</i> sp.	2:3, 2:0, 1:2,
Campichoetidae	<i>Pareuthyshaeta electrica</i>	2:6, 1:1
Campichoetidae	<i>Pareuthyshaeta minuta</i>	1:2, 2:0
Campichoetidae	<i>Pareuthyshaeta</i> sp.	2:2
Chloropidae	<i>Protoscinella electrica</i>	2:1 + 1 Acroceridae, 2:0, 2:0, 2:0, 2:0, 0:2
Chyromyidae	<i>Gephyromyiella electrica</i>	1:2
Cypselosomatidae	<i>Cypselosomatites succini</i>	1:1 in copula
familia inc.sed.	gen.sp.	6
Heleomyzidae	<i>Protoorbellia hoffeinsorum</i>	2:0
Heleomyzidae	<i>Suillia major</i>	0:1 + 0:1 Camillidae + 1:0 inc. sed.
Heleomyzidae ?	gen.sp.	0:4
Megamerinidae	<i>Palaeotanypeza spinosa</i>	0:1 + 0:1 <i>Palaeotimia thoesti</i> ,
Dryomyzidae		
Micropezidae	<i>Electrobata tertaria</i>	0:3
Milichiidae	gen.sp.	1:3, 4:0
Proneottiophilidae	<i>Proneottiophilum extinctum</i>	0:4 + 2 + 1:0 + 1:0 Heleomyzidae (coupl. 89b)
Psilidae	<i>Electrochyliza succini</i>	2:0
Sciomyzidae	gen.sp.	2:1

**Table 2:** Species of acalyptates identified from both deposits, Baltic and Bitterfeld.

Anthomyzidae	<i>Protanthomyza collarti</i>
Camillidae	<i>Protocamilla succini</i>
Campichoetidae	<i>Pareuthyshaeta electrica</i>
Chloropidae	<i>Protoscinella electrica</i>
Cryptochaetidae	<i>Phanerochaetum tuxeni</i>
Diopsidae	<i>Prosphyracephala succini</i>
Drosophilidae	<i>Electrophortica succini</i>
Heleomyzidae	<i>Electroleria alacris</i>
Heleomyzidae	<i>Suillia major</i>
Heleomyzidae	" <i>Heteromyza</i> " <i>dubia</i>
Milichiidae	<i>Phylloomyza jaegeri</i>
lopteridae	<i>Pallopterites electrica</i>
Proneottiophilidae	<i>Proneottiophilum extinctum</i>
Pseudopomyzidae	<i>Eopseudopomyza kuehnei</i>
Psilidae	<i>Electrochyliza succini</i>

Thus they may be overlooked or allocated wrongly. In the figure of HENNIG they were omitted. The holotype is embedded in lateral position, became blackish and is enfolded in iridescent fissures, the prsc are masked. In the series they rarely are absent but, if present, they always insert adjacent to the edge of scutellum. — Absent: apomorphic.

(13) Fig. 314 in HENNIG's monograph (l.c.) shows a small setula between the vertical bristles vte and vti, rarely to be observed in acalyptates. In our series this setula mostly inserts in the same position, rarely outside of the vte. — Position without judgement.

(14) Eyes of *P. electrica* are mostly covered by dense long pubescence confirmed also for the holotype. Some specimens only possess dense short pubescence, in some others these fine microchaetae cannot be detected. Both conditions occur in extant species of the sister genus *Tricimba*. — Judgement uncertain.

(15) Cerci (posterior appendages in the male epandrion) were not described by HENNIG as the sex of the holotype could not be ascertained by him. One of us (M.v.T.) identified it as a female. All our males, 50% of all specimens, possess large-scaled rounded cerci with long hairs around their edge. Their outline, well to be seen in lateral view, shows slight variation towards a more acute lower posterior end in some few specimens. — Not evenly rounded: apomorphic.

(16) The length of body and wing of each specimen (24♂♂, 21♀♀) was measured. With one exception the ratings show a Gaussian distribution: Body (without ovipositor and antennae): 1.52-2.52 mm, on average 2.06 mm; wing 1.35-2.03 mm, on average 1.70 mm. One well preserved female with identical morphology is placed far outside these ranges: body 3.11 mm, wing 2.40 mm. — The normality in 44 specimens supports that only one species is involved. Extreme sizes, short or long, are not connected with plesiomorphic or apomorphic conditions of other characters.

Palaeontologists working with marine or freshwater organisms and their rich material of transformation series from much longer lasting geological periods will not understand our enthusiasm. But terrestrial animals normally underlie quicker changes of climate conditions and other unbuffered catastrophic events. Their fossil record is always extremely poor. For a dipterist confronted with the tremendous difficulties in species separation of our present fauna *P. electrica* is an impressive example for the slow evolutionary process of altering minute characters all appearing to be independent from one another. Finally the discussed transformation series ended in at least one further *Protoscinella*-species (with much smaller 3<sup>rd</sup> antennal segment, different cerci and other reductions) and the first detected fossil *Tricimba*-species (with all characters of extant *Tricimba*-species, except a present sa-bristle of the fossil) both included in our key. Hundreds of extant *Tricimba*-species are distributed worldwide, which in a large extend are still undescribed. The never-ending discussion about whether genera of the Tertiary age are surviving to date can be answered without hesitation: Yes! *Protoscinella* and the mentioned millipede and spider genera from Baltic amber are best examples.

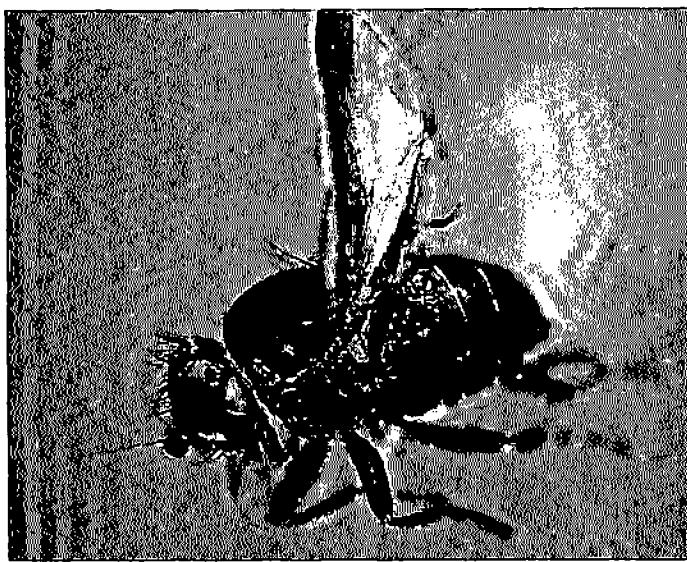


Fig. 15: Milichiidae, *Phylloomyza* sp., ♂, body 1.8 mm, lateral habitus; det. I. Brake; coll. HOFFEINS 878-3.



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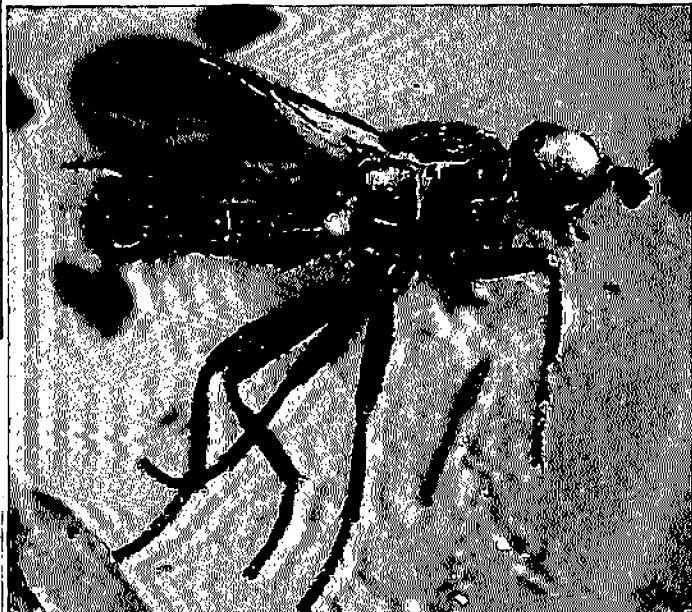


Fig. 18: Pyrgotidae, undescribed species, ♂, body 4.1 mm, lateral habitus; coll. HOFFEINS 1284-2.

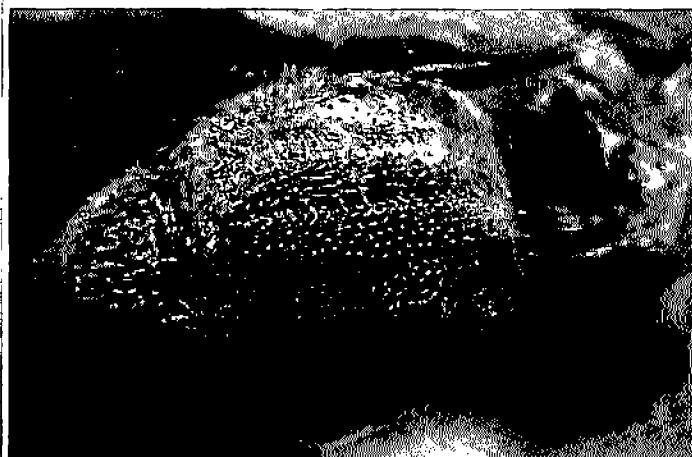


Fig. 19: Chloropidae, *Protoscinella electrica* HENNIG, ♀, body 2.5 mm, length of mesonotum 0.8 mm, mesonotum and scutellum in dorsal view showing the typical three central impressed grooves with "criss-cross"-arranged acrostichal setulae and short macrochaetae; compare chapter variability; coll. HOFFEINS 964-2.

Fig. 16-17: Pyrgotidae, undescribed species, ♂, body 4.1 mm; lateral habitus and details of left mid tibia with extended tibial spur. Specimen from autoclaved amber, frontal part with important characters of head partly obscured by translucent resin layers; coll. HOFFEINS 1284-1.

- 41 (40) Each side 3 or more fronto-orbitals present (II, fig. 19).
- 42 (43) Presutural bristle absent or a weak one present (I, fig. 185). Postvertical bristles divergent (I, fig. 182, 183). Vibrissae present, 3 pairs of scutellar bristles, posterior crossvein shorter than end-section of  $m_{3+4}$ .
- 2<sup>nd</sup> antennal segment with triangular projection at outer surface ..... *Electroclusiodes meunieri* (HENDEL), Clusiidae
- 42a 3<sup>rd</sup> antennal segment very small and slightly sunken in 2<sup>nd</sup> article, higher than long, arista terminal, anal cell rudimentary, prs inserts very low; 0 vi, 4 ors, oc proclinate, pvt divergent, 0 m, 2 dc prsc, ipa probably absent, 4 rows of acr., all t with dpr, genae bent under, wing 2.15 mm ..... sp.n. 65, ?Clusiidae
- 42b Anterior and longest one of 4 ors bent inwards, 2<sup>nd</sup> antennal segment with triangular extensionis at outer surface, prsc small or missing. Species is similar to *E. meunieri* ..... sp.n. 66, *Electroclusiodes* sp., Clusiidae
- 42c Anterior one or two of 3 ors bent inwards, posterior one bent back- and outwards, pvt absent, costa ends at  $r_{4+5}$ ;  $r_{2+3}$  and  $r_{4+5}$  strongly convergent towards end, nearly touching posterior cross vein absent; oc upright, 0 prs, 1 pp, 1 m, 1 st, 2 dc 0 prsc, ipa absent, 4-5 rows of acr, ap widely separated,  $f_1$  with 1 bristle in basal ventral position, body and wing 1.99 mm (Baltic and Bitterfeld amber) ..... sp.n. 67, ?Carnidae
- 42d Try also couplet 43a with very peculiar characters but unknown pvt-character.
- 42e Outside of 2<sup>nd</sup> antennal segment with triangular projection at outer surface, clypeus prominent, 4 ors, 3 pp, 3 pairs of scutellars (one on the disc); vi, 2 prolonged if above lunule, pvt divergent, 2 d, 2 m (lower short), 1-2 st, prsc, 10 rows of acr, all f bare, all t without dpr, subcostal break, body/wing 3.56-4.15/2.96-3.41 mm ..... sp.n. 68, *Electroclusiodes*, Clusiidae
- 42f Length of 3<sup>rd</sup> antennal segment nearly 2-times its height, subcosta complete, bent towards subcostal break in an angle of 100°, subcostal cell large, pvt parallel, 6-7 ors, oc short, 3 pp, 2 sa (the anterior also called praearalar); vi, prs weak or absent and near notopleuron, ia, 2 la, all t with dpr, wing 4.88 mm. If m is judged to be short (couplet 39), then go to couplet 79 ..... sp.n. 69, ?Sciomyzidae
- 42g Head round, 2<sup>nd</sup> antennal segment with triangular projection at outer surface, legs relatively long; 3 ors, pvt divergent, 0 prs, 4 dc, prsc, 3.8 mm ..... sp.n. 70
- 42h 4 ors, posterior crossvein stands far basally on  $m_{3+4}$ ; vi, 0 prsc, 2 dc ..... sp.n. 71
- 42i Small species, ap long and widely separated, genae below eyes narrow, small spinulae along costa; vi, pvt convergent, 1 st, 3 dc, prsc, no prominent bristle on  $f_1$  ..... sp.n. 72
- 42k Short costal spinules in even distances,  $r_1$  long ending near mid of wing,  $r_{4+5}$  conspicuously bent backwards, at its end parallel with  $m_{1+2}$ ; vi, 3 ors, pvt divergent, 0 prs, 1 long pp, 1 m, 2 st, 2 dc, prsc, at least  $t_1$  without dpr, body/wing 3.56/3.12 mm ..... sp.n. 73, ?Heleomyzidae
- 42l Body/wing 2.28/2.35 mm, occiput (back of head) concave, eye covers whole head side, vi and h absent; 3 weak ors, weak proclinate oc, pvt weak, upright-proclinate, tiny pp, 1 m, 1 st, 2 dc, 0 prsc, 4 rows of acr, all f bare, all t without dpr, 1 spur at end of  $t_2$ , femora very slender, sc and  $r_1$  near together, jowl below eye linear, 3<sup>rd</sup> antennal segment slightly longer than high with prolonged pubescence ..... sp.n. 74
- 42m Body and wing both 2.78 mm, 3<sup>rd</sup> antennal segment relatively large, 3 long ors, 1 long pp, meso- and sternopleuron densely pilose; vi, oc long, pvt short, convergent-crossed, 2+1 small m, 1 st, 3 dc, (probably prsc),  $t_2$  with 1+3 terminal spurs ..... sp.n. 75
- 42n Ocelli close together, pvt divergent, long, sockets touching themselves, prs absent, small costal spinules in narrow distances, 4 scapular bristles in transverse row; vi strongly convergent, 3 ors, oc extremely long, central occiput with dense group of setulae, 1 m + 7 small bristles, 2-3 dc, scutellum large, prsc, at least  $t_1$  and  $t_2$  with dpr,  $t_1$  with cleaning comb,  $t_2$  with spur at end, mt, with cleaning brush basally, body/wing 4.78/3.90 mm ..... sp.n. 76
- 42o 5-6 ors, the 2 or 3 anterior ones bent inwards,  $r_1$  ends near mid of wing, pvt upright- divergent; oc small, 4 small reclinated m, 4 st, 5 dc (the 2 anterior ones very small), ap relatively near together, jowl below eye bent under, 3<sup>rd</sup> antennal segment round, black, body/wing 2.68/2.39 mm ..... sp.n. 77
- 43 (42) Presutural bristle present (prs; I, fig. 142, 231, 256). Postvertical bristles (pvt) convergent (I, fig. 139, 140, 228, 254).
- 43a (The pvt are not visible, probably they are absent). One ocellus only, claws very short and not evenly curved but bent over in an abrupt angle of 90°, parallel and closely approximated, pulvilli braced sideways (see text); ors long and weak, 7-8 ors: 3 posterior reclinate and 4 (one side 5) anterior (inserted anteriorly of ocellar triangle) inclinate, oc short and divergent, pp not detectable, if present then they are very

- short, 1 st,  $t_3$  with dpr,  $t_2$  with very long apical spur and one shorter spur, subcostal break, short 2<sup>nd</sup> antennal segment (!), mid coxal prong absent, body 4.1 mm ..... sp.n. 78, Pyrgotidae
- 43b Four reclinate ors, 3 lower inclined ori, 2 pairs of long if, 4 st, 2m, face with antennal pits, epandrium round with large-scaled surstyli and gonites ..... sp.n. 79
- 43c Three reclinate ors, antennae in deep foveae, behind vti a further convergent bristle, vi bent inwards, 0 st, oviscape. Compare couplet 56a ..... sp.n. 80, Meoneurites sp., Carnidae
- 44 (45) Sternopleuron with 3 long and strong sternopleural bristles along upper margin (I, fig. 144). Each side 4 fronto-orbitals (ors), the anterior one is bent inwards (I, fig. 139, 140). Vibrissae absent (I, fig. 138). Intraalar bristle (ia) present (I, fig. 142) ..... *Hemilauxania incurviseta* HENNIG, Lauxaniidae
- 44 a 6 ors, 1 ia, 2 sa (= 1 sa + 1 praearalar), 2 la. Go to couplet 42f.
- 45 (44) Sternopleuron with only 1 or 2 long and strong sternopleural bristles (I, fig. 230, 256). Each side only 3 ors (I, fig. 227, 228, 254, 255). The ia bristle absent. Vibrissae present (I, fig. 227, 229, 255).
- 45a 2 st, 4-5 ors (the anterior one probably inclinate), 2 h, axillaris ( $a_2$ ) distinct but not reaching wing margin; pvt convergent, 2 m, 3 dc (the 2<sup>nd</sup> and 3<sup>rd</sup> small and near to the 1<sup>st</sup>), prsc, no bristle or spine on lower side of  $f_1$ , 1 small dorsal bristle on  $f_2$ , at least  $t_1$  and  $t_2$  without dpr, subcostal cell weakly dark sclerotized, epandrium with about 4 strong upright dorsal bristles ..... sp.n. 81
- 45b 6 ors, at least the 2 hind ocelli present (anterior one invisible),  $t_2$  without apical spur ..... sp.n. 82, Pyrgotidae
- 45c Go back to couplet 43a.
- 46(47) Anterior fronto-orbital bristle bent inwards (I, fig. 228). 1<sup>st</sup> femur without a ventral spine ..... *Gephyromyiella electrica* HENNIG, ?Chyromyidae
- 47(46) Anterior fronto-orbital bent backwards like the further ones (I, fig. 254, 255). 1<sup>st</sup> femur with a ventral spine (I, fig. 257), a specimen in the coll. HOFFEINS with thinner and more basal spine ..... *Protanthomyza collarti* HENNIG, Anthomyzidae
- 47a As 47 but 1<sup>st</sup> femur without ventral spine, arista bare; mesonotum humped, clypeus prominent, sc ends near  $r_1$ ,  $t_1$  cleaning-comb absent; 3 m ..... sp.n. 83
- 47b 1<sup>st</sup> femur with ventral spine, mesonotum normal,  $t_1$  with apical cleaning comb, sc ends distinctly separate from  $r_1$  ..... sp.n. 84
- 47c Clypeus normal,  $t_1$  without and  $t_3$  with a cleaning comb, ap wide apart; vi small, oc long, pvt short and crossed-proclinate; 1 pp, mesopleuron with long hairs, 2-3 m, 1 st, 4 dc, prsc long,  $f_1$  with 5 dorsal and 10 ventral bristles,  $f_2$  with 2 anterolateral bristles, subcostal cell darkened-sclerotized, sc thickened at end, ends near  $r_1$ , genae below eye linear, body/wing 3.27/2.98 mm ..... sp.n. 85
- 48 (39) Mesopleuron without prolonged strong bristles at hind margin. Moreover the mesopleuron is bare or (rarely) finely haired (but compare 49 and 84: very finely haired).
- 48a Large species (body estimated 6.2 mm), costa with spinules, subcostal cell dark; h, 2 n, prs, 1 pp, 0 m, 1 st, 3-4 dc (4<sup>th</sup> small), prsc, ap longer than la (compare couplet 14),  $f_1$  with 1 anterolateral and 4 long and further weak ventral bristles, all t with dpr, strong femora, long  $r_1$  ..... sp.n. 86, ?*Proneottiophilum*, Proneottiophilidae
- 48b Scutellum flat above (not convex), 1 dc and prsc tiny ..... sp.n. 87
- 49 (50) Each side only 1 fronto-orbital bristle present (II, fig. 10). Vibrissae absent, h and prsc present, size variable, wing 1.76-3.66 mm ..... *Morgea mcalpinei* HENNIG, Pallopteridae
- 49a Spinules along costa, pp and h and prsc absent, sc ends far from  $r_1$ ; vi, 1 ors, pvt long and parallel, prs, 0 m, 1 st, 2 dc,  $f_2$  anteriorly with 1 bristle in distal third, all t with dpr, genae as broad as 3<sup>rd</sup> antennal segment high, body/wing 4.68/5.51 mm. Similar to couplet 49h ..... sp.n. 88, ?Sciomyzidae
- 49b 3<sup>rd</sup> antennal segment distinctly longer than high, vi and ors and oc absent, pvt convergent and widely apart, 1 short dc very near to scutellum. Go to couplet 61.
- 49c Pectinate arista (rays on both sides), many strong peristomal bristles, 2<sup>nd</sup> antennal segment cap-like, clypeus prominent, proboscis large, prsc absent ..... sp.n. 89, Periscelididae
- 49d Clypeus very prominent, costal spinules, h absent; vi, 1 ors and 8 reclinate orbital setulae, oc long, pvt parallel, 0 m, 1 st, 2 dc, 0 prsc,  $f_2$  with 1 strong anteroventral bristle, all t with dpr, subcostal break, axillaris present, jowl bent under the eye, as broad as 3<sup>rd</sup> antennal segment, wing 3.56-4.88 mm ..... sp.n. 90, ?Sciomyzidae
- 49e Clypeus prominent, costal spinules absent, h and prs present; 0 vi, 1 ors, oc long, pvt long divergent, prs, 1 pp, 0 m, 2 st, 2 dc, 0 prsc,  $f_1$  with 7 dorsal and 3 strong/9 weak ventral bristles,  $f_2$  bare,  $f_3$  distally ventral

- with 2 strong bristles, subcostal cell dark sclerotized, subcostal break, genae narrow, equal with diameter of  $t_1$ , oviscape, epandrium with acute projection, wing 3.90-4.00 mm ..... sp.n. 91, *Morgea* sp., Pallopteridae
- 49f Clypeus prominent, costal spinules absent, h present, prs absent; vi tiny, 1 long ors, long oc, short divergent pvt, pp probably absent, 0 m, 1 st, 2 dc 0 prsc, all f seem to be bare,  $t_1$  with dpr and terminal cleaning comb, 3<sup>rd</sup> antennal segment small, wing 3.12 mm ..... sp.n. 92
- 49g Clypeus very prominent, bent upwards, costal spinules short, close together, separated by normal setulae, 1 h and 2 st present; vi very long and thin basally, oc long and upright-parallel, pvt convergent, 0 pp, 0 m, 2 st, 2 dc, 0 prsc, sockets of ap wide apart,  $f_1$  with 2 dorsal bristles (one basal and one distal),  $f_2$  with 1 long anterolateral bristle in distal half,  $t_2$  with and  $t_3$  without dpr,  $r_1$  short,  $r_{2+3}$  long, a small sclerotized plate below female cerci, wing 3.27 mm ..... sp.n. 93
- 49h Costal spinules present, 0 h, 1 st, prs, 0 prsc; vi, 1 or, oc long, setulae on mesopleuron, 1 st, 2 dc, 6 rows of acr, jowl bent under the eye, 3<sup>rd</sup> antennal segment small, wing 4.00 mm. Similar to couplet 49a, genae narrower ..... sp.n. 94, ?Sciomyzidae or ?Heleomyzidae
- 49i Tiny species, body/wing 1.79/1.71 mm, face convex (artificially?), the following bristles are absent: pvt, vti, prs, pp, m, st, ia, epa, ipa, sa, prsc, head broader than thorax, 3<sup>rd</sup> antennal segment very short, arista inserted basally, very long and thin; vi, 1 long ors in front of which is a row of 3 meticulous setulae, oc long proclinate, vte, all four bristles 1 h and 1+1 n and 1 h very short, mesopleuron without hairs, sternopleuron with 5 fine hairs, 1 dc, only 2 rows of acr consisting of 4 setulae each, ap upright, all f bare, all t without dpr,  $t_1$  with cleaning comb, long bristle at end of  $t_2$ ,  $r_1$  long,  $r_{2+3}$  short ending nearer to  $r_1$  than to  $r_{4+5}$ , sc bent steeply to costa, costa-break absent, genae linear in front, very broad at rear, huge looped aedeagus with dense long setulae ..... sp.n. 95, ?Aulacigastridae or ?Periscelididae
- 50 (49) Each side at least with 2 fronto-orbitals (attention: couplets 60 and 61 of HENNIG includes text and one species without ors).
- 51 (60) One or more fronto-orbitals bent inwards (I, fig. 238, 245, 246, 273; II fig 35, 46).
- 52 (53) Postvertical bristles convergent (II, fig. 35, 36) or at least parallel [key of HENNIG 1971].
- 52a(52b) Each side 3 upper fronto-orbitals present, all bent outwards (over the edge of eye) ..... [the valid taxon:] *Phyllomyza juegeri* HENNIG, Milichiidae
- 52b(52a) Each side only 2 fronto-orbitals present, which are bent outwards, as well 2 anterior ors bent inwards ..... *Pseudodesmometopa succineum* HENNIG, Milichiidae
- 52c Upper 2 ors bent upwards and outwards (or the anterior only outwards), lower 2 ors bent inwards, proboscis strongly elongate and acute, palpi long and thick; vi, 2 rows of reclinate interfrontals, the anterior pair proclinate, small divergent oc, small widely separated convergent pvt, 1 pp, 0 m, 1 st, 2 dc, prsc, 8 rows of acr,  $f_1$  with 2 dorsal setae, a ventral spine, and 10 posteroventral bristles in row,  $f_2$  bare, all t with dpr, costa ends at  $m_{1+2}$ , sc as a fold towards costa-break near  $r_1$ , anal cell rudimentary, analis absent, axillaris present, face concave with keel between 1<sup>st</sup> antennal segments, 3<sup>rd</sup> antennal segment ball-like, body/wing 1.66-2.08/1.22-1.76 mm ..... sp.n. 96, *Pseudodesmometopa* sp., Milichiidae
- 52d Upper 3 ors bent backwards, one anterior ors (widely separated from the upper) bent inwards, proboscis strongly elongate, palpi short; vi, if on yellow frons all proclinate, a pair of convergent anterior ones long, 2/3<sup>rd</sup> of their length crossing the lunule, oc long, pvt parallel, vertex with 4 small inclined bristles behind pvt till pvt, 0 pp, 0 m, 2 dc, 2 st, sternopleuron haired, prsc, ipa absent, 10 rows of acr,  $f_1$  posterodorsal with 8 bristles,  $f_2$  with 1 long posterodorsal bristle in distal third,  $r_1$  relatively long, subcostal cell light and narrow, alula present, face with deep foveae and broad keel, 3<sup>rd</sup> antennal segment slightly higher than long, together with 1<sup>st</sup> and 2<sup>nd</sup> one yellow with prolonged upwards directed pubescence, body and bristles yellow except one dark n, body/wing 1.88/2.03 mm ..... sp.n. 97, Milichiidae
- 52e Two upper ors bent backwards and outwards, 1 lower inclinate ors, proboscis moderately elongate, labelum with deep incisure, ending in two narrow tips with only 1 or 2 pseudotracheae each side, palpi not elongate, widened distally ..... sp.n. 98
- 53 (52) Postverticals (pvt) divergent or absent.
- 54 (55) Only 2 fronto-orbitals present, the anterior one bent inwards, the posterior backwards (I, fig. 238). Mouth edge protruding (I, fig. 240). (Hind edge of head peculiarly excavated. Postvertical bristles absent. Mesopleuron with fine hairs). Arista more or less bare, vte and vti present ..... *Protaulacigaster electrica* HENNIG, Aulacigastridae

- 54a Similar to preceding species, but arista pectinate with dorsal and ventral rays, pvt and vti absent, instead of them small proclinate bristles present; 2 n, prs and prsc absent, ap and la, costa without break, small species. (Species runs also to 5d) ..... sp.n. 99, ?Aulacigastridae
- 54b Clypeus prominent, 2<sup>nd</sup> antennal segment cap-like, 5 ors, the 2 anterior ones inclinate, f<sub>1</sub> bristled on lower side; 2 dc ..... sp.n. 100, ?Aulacigastridae
- 55 (54) Four fronto-orbitals present. Mouth-edge not protruding, postverticals divergent (in *Anthoclusia* they are developed only as very fine hairs).
- 56 (57) Antennae embedded in deep foveae (I, fig. 274) [this character is supervalue]. Each side of scutellum with 3 bristles (I, fig. 278). Genae in front with only one long and strong vibrissa (I, fig. 275, 276). Compare couplets 42c, 42d. Female cerci fused [discussed by HENNIG, confirmed by M.v.T.] ..... Meoneurites enigmatica HENNIG, Carnidae
- 56a As couplet 56 but scutellum with 2 pairs of bristles only, both bent backwards, female cerci very narrow, if fused not visible. Compare couplet 43c ..... sp.n. 101, Meoneurites sp., Carnidae
- 57 (56) Antennae not embedded in foveae. Each side of scutellum with 1 or 2 bristles. Each side of genae in front with about 4 equally long and equally strong bristles (I, fig. 246). If only 2 equal bristles present go to couplet 59a.
- 57a Genae broad, eyes oval, 3 pairs of scutellar bristles, vi and 9 fine peristomal setae ..... sp.n. 102, Clusiidae
- 57b Each side of pvt a further convergent bristle, 3 pairs of scutellars, h, 2 n, prs, 2 dc, sc complete ..... sp.n. 103
- 58 (59) In the wing venation the distance between r<sub>2+3</sub> and r<sub>4+5</sub> is shorter than the distance between the ends of r<sub>4+5</sub> and m<sub>1+2</sub> (I, fig 250). Each side of scutellum with 1 lateral and 1 apical bristle (I, fig 248). Prescutellar bristles (prsc) present (I, fig 248). Species runs also to couplet 73, comment see there ..... Anthoclusia gephyrea HENNIG, Neurochaetidae
- 59 (58) In the wing venation the distance between r<sub>2+3</sub> and r<sub>4+5</sub> is about 1½ the length of the distance between the ends of r<sub>4+5</sub> and m<sub>1+2</sub> (III, fig. 31). Each side of scutellum with 1 (the apical) bristle only. Prescutellars (prsc) absent. 2 ors reclinate and 2 ors inclinate, 3<sup>rd</sup> antennal segment with long pubescence, vi + 3 peristomal bristles ..... Anthoclusia remotinervis HENNIG, Neurochaetidae
- 59a Similar to 59, but 3<sup>rd</sup> antennal segment and arista with short pubescence, vi and 1 peristomal bristle, ventral side of f<sub>1</sub> with 8 spinules and 6 bristles ..... sp.n. 104
- 59b Similar to 59, but 3<sup>rd</sup> antennal segment small, 3 reclinate and 1 inclinate ors, 0 prs, mesopleuron only hairy, 2 dc, t without dpr, 0 prsc, ap and only 1 small la ..... sp.n. 105
- 60 (51) All fronto-orbital bristles (if such present at all) bent backwards (reclinate).
- 61 (62) Vertical- and fronto-orbital bristles absent. Head only with one pair of small convergent bristles present behind ocellar triangle (I, fig. 267A; III, fig. 42). Arista very short, shorter than the elongate and downwards directed 3<sup>rd</sup> antennal segment (I fig. 266A). Compare couplet 49b ..... Phanerochaetum tuxeni HENNIG, Cryptochetidae
- 62 (61) Vertical bristles (at least 1 pair), fronto-orbital bristles (at least 2 pairs), and postvertical bristles all present. Arista of normal size: longer than the roundish or short-elliptic 3<sup>rd</sup> antennal segment.
- 62a Large fly, go back to couplet 36a.
- 63 (70) Neither humeral (h) nor presutural bristle (prs) present. Postvertical bristles (pvt) always divergent. [Disagreement with I, fig. 1, parallel/convergent, fig. according with specimens in the von TSCHIRNHAUS-collection, and also with couplet 68-69, parallel].
- 63a Go to couplet 70a.
- 64 (65) Each side only 2 fronto-orbital bristles present (III, fig. 37, 38), in front of them 5 very short orbital setulae in row. Postvertical bristles (pvt; III, fig. 37) very short and fine. Wing venation: subcostal vein not reaching the costa (III, fig. 33); vein r<sub>2+3</sub> short, ending half way between r<sub>1</sub> and r<sub>3+4</sub>. Small species (body-length about 2 mm) ..... Succinasteia carpenteri HENNIG, Asteiidae
- 64a Similar to preceding, r<sub>2+3</sub> ends very near to r<sub>1</sub>, 2 rows of acr ..... sp.n. 106, Astiosoma sp., Asteiidae
- 65 (64) Each side 3 or 4 fronto-orbital bristles present. Postvertical bristles long and strong. Subcostal vein always reaching the costa. Larger species (body length at least 5 mm).
- 66 (67) Costa at ending of sc with break (I, fig. 11). Short reclinate ocellar bristles present, as well each side 4 fronto-orbital bristles (ors) (I, fig. 7, 8), the most upper one far behind ..... Cypselosomatites succini [sic!, corrected printing error] HENNIG, Cypselosomatidae

**Table 5: Survey via parts of the studied Acalyptratae with complete scientific names. Material studied by HENNIG included for comparison only, signed with •; E = EICHMANN, G = GRÖHN, Ho = HOFFEINS, K = KERNEGGER, L = LUDWIG, vT = VON TSCHIRNHAUS, T = TEUBER.**

Family	Key	Species	•	E	G	Ho	K	L	T	vT	Σ
Acartophthalmidae	30	<i>Acartophthalmites tertaria</i> HENNIG, 1965	5		1	11				3	20
	—	sp.					1				1
Anthomyzidae	47	<i>Protanthomyza collarti</i> HENNIG, 1965	2			4				2	8
	74d	sp.								1	1
Astiidae	64	<i>Succinasteia carpenteri</i> HENNIG, 1969	1			4				2	7
	64a	<i>Astiosoma</i> sp.								1	1
	25a	sp.				1					1
Aulacigastridae	54	<i>Protaulacigaster electrica</i> HENNIG, 1965	1								1
	6a	sp. 1					1			1	2
	49i	sp. 2								1	1
	54a	sp. 3								2	2
	54b	sp. 4								1	1
Camillidae	51	<i>Protocamilla groehni</i> GRIMALDI, 2008			1						1
	6	<i>Protocamilla succini</i> HENNIG, 1965	7			22				12	41
	—	<i>Protocamilla</i> sp.			1						1
	→	2-3 spp.: partly included in couplets 5b, 5g, 5i				1	2			3	6
Campichoetidae	9	<i>Pareuthyshaeta electrica</i> HENNIG, 1965	11			7	2	1		28	49
	8	<i>Pareuthyshaeta minuta</i> MEUNIER, 1904	1		1	16				7	25
	9a	<i>Pareuthyshaeta</i> sp.								7	7
	5h	sp. 1					1			1	2
Carnidae	56	<i>Meoneurites enigmatica</i> HENNIG, 1965	2							1	3
	56a	<i>Meoneurites</i> sp. 1				1				1	2
	43c	<i>Meoneurites</i> sp. 2								1	1
	42c	sp.				1					1
Chamaemyiidae	77	<i>Procremifanía electrica</i> HENNIG, 1965	2	3		3				1	9
	77a	<i>Procremifanía</i> sp.			1						1
	40a	sp.		3		2	3			3	11
Chloropidae	32	<i>Protoscinella electrica</i> HENNIG, 1965	1		3	21	5			16	46
	32b	<i>Protoscinella</i> sp.					1			2	3
	72a	<i>Tricimba</i> sp.								1	1
Clusiidae	42	<i>Electroclusioides meunieri</i> (HENDEL, 1923)	4	1	3	6				17	31
	34	<i>Electroclusioides radiospinosa</i> HENNIG, 1965	1			3	1			1	6
	42b	<i>Electroclusioides</i> sp. 1								2	2
	42e	<i>Electroclusioides</i> sp. 2								3	3
	74	<i>Xenanthomyza larsoni</i> HENNIG, 1967	1			1				5	7
	→	9 species: 33b, 42a, 57a, 73a, 74a, 74b, 74c, 74e, 79f		1	2	7	8			15	33
? Clusiidae	—					2					2
Conopidae	2c	<i>Hoffeinsia baltica</i> STUKE, 2005				1					1
	2b	<i>Palaeomyopa hennigi</i> STUKE, 2003									0
	2a	<i>Palaeomyopa tertaria</i> MEUNIER, 1912	2			1				1	3
	2d	sp.								1	1
Chyromyiidae	46	<i>Gephyromyiella electrica</i> HENNIG, 1965	2			3	1				6
	—	sp.				2					2
Cryptochetidae	61	<i>Phanerochaetum tuxeni</i> HENNIG, 1965	2		2	2	2		1	5	14
Cypselosomatidae	66	<i>Cypselosomatites succini</i> HENNIG, 1965	1		1	3	1			1	7
Diopsidae	1	<i>Prosphyracephala succini</i> (LOEW, 1873)	2	1	1	4		1	1		10
	2	sp.						1			1
Drosophilidae	4	<i>Electrophorтика succini</i> HENNIG, 1965	1			9	3			6	19
	4b	<i>Electrophorтика</i> sp. 1								5	5
	4c	<i>Electrophorтика</i> sp. 2								7	7
	—	sp.					1	1			2
Dryomyzidae	85	<i>Palaeotimia lhoesti</i> MEUNIER, 1908	1			1					2
	37	<i>Prodryomyza electrica</i> HENNIG, 1965	2		1	6	1			4	14
	37a	sp.						1		1	2
Heleomyzidae	91c	<i>Balticoleria michaeli</i> WOZNICA, 2007								1	1
	92	<i>Chaetohelomyza electrica</i> HENNIG, 1965	4			1				1	6
	89	<i>Electroleria alacris</i> (MEUNIER, 1904)	8	2	1	19	12			9	51
	—	? <i>Electroleria</i> sp.			1		6				7
	91,92c	"Heteromyza" <i>dubia</i> MEUNIER, 1904	4	1	2	7	3			9	26

Table 5: continued

Family	Key	Species	•	E	G	Ho	K	L	T	vT	Σ
	19d	<i>Paleohelomyza kotejai</i> Woźnica & Palaczyk, 2005				1				1	2
	16n	<i>Protoorbellia hoffeinsorum</i> Woźnica, 2006				2					2
	19	<i>Protosuillia media</i> (Meunier, 1904)	4			2	2			5	13
	18	<i>Suillia major</i> Meunier, 1904	4		8	18	7	7		16	60
—		Heleomyzinae species				2					2
—		Suillinae species				20	2				22
→		sp. 16f, 42k, 88e			3	8				5	16
? Heleomyzidae	—					3					3
Lauxaniidae	87	<i>Chamaelauxania succini</i> Hennig, 1965	3		1	3	1			10	18
—		<i>Chamaelauxania</i> sp.				3					3
	44	<i>Hemilauxania incurviseta</i> Hennig, 1965	2		1	5	3			6	17
—		<i>Hemilauxania</i> sp.				2					2
→		species (partly to be included in couplet 79c)		1	1	6	2			3	13
Megamerinidae	24	<i>Palaeotanypeza spinosa</i> Meunier, 1917	1		1	4				2	8
—		sp.				1					1
Micropesidae	69	<i>Electrobata tertiaria</i> Meunier, 1909	4		1	7				2	14
	68	<i>Electrobata myrmecia</i> Hennig, 1965	2			1				1	4
	68a	<i>Electrobata</i> sp. 1								1	1
	68b	<i>Electrobata</i> sp. 2								1	1
	68c	<i>Electrobata</i> sp. 3			1					1	1
	75a	sp. 1								1	1
—		sp.	1			1					2
Milichiidae	52a	<i>Phylloomyza jaegeri</i> Hennig, 1967	2			9	2	1		2	16
	52b	<i>Pseudodesmometopa succineum</i> Hennig, 1971	1							2	3
	52c	<i>Pseudodesmometopa</i> sp.								2	2
→		sp. (partly to be included in couplet 52d)				11				1	12
Natalimyzidae	4a	<i>Natalimyza</i> sp.				1				1	2
Neurochaetidae	58,73	<i>Anthoclusia gephyreia</i> Hennig, 1965	2		2	4				2	10
	59	<i>Anthoclusia remotinervis</i> Hennig, 1969	1			5				1	7
—		sp.				5					5
Odinidae	15	<i>Protodinia electrica</i> Hennig, 1965	1		3	8	1			7	20
—		sp.				1					1
Pallopteridae	16	<i>Pallopterites electrica</i> Hennig, 1967	1			4		1		3	9
	40	<i>Glaesolonchaea electrica</i> Hennig, 1965	2			4	3			5	14
	49	<i>Morgea mcalpinei</i> Hennig, 1967	1			3	1			5	10
	49e	<i>Morgea</i> sp.								2	2
	16a	sp.				2	1			4	7
Periscelididae	5k	<i>Procyamops succini</i> Hoffeins & Rung, 2005				1					1
	24a	sp. 1								2	2
	49c	sp. 2								2	2
Joneottiophilidae	14	<i>Proneottiophilum extinctum</i> Hennig, 1969	1			11				12	24
	14b	<i>Proneottiophilum</i> sp. 1				1				2	3
	48a	<i>Proneottiophilum</i> sp. 2								2	2
Pseudopomyzidae	17a	<i>Eopseudopomyza kuehnei</i> Hennig, 1971	1		1	8	2			7	19
—		sp.				4					4
Psilidae	25	<i>Electrochyliza succini</i> Hennig, 1965	7	1	1	10				15	34
—		sp.			1		1	1			3
Pygotidae	43a	sp. 1					1				1
	45b	sp. 2					1				1
Sciomyzidae	36	<i>Prophaeomyia loewi</i> Hennig, 1965	4			7	3	1		1	16
	84	<i>Palaeoheteromyza curticornis</i> Hennig, 1965	3								3
	80	<i>Prosalticella succini</i> Hennig, 1965	2		3	9				1	15
	21	<i>Palaeoheteromyza crassicornis</i> Meunier, 1904	2			3					
	82	<i>Palaeoheteromyza investiganda</i> Hennig, 1965	1			2					3
	76	<i>Sepedonites baltica</i> Hennig, 1965	2			1					3
→		spp. 16b 21a 36a 42f 49a 49d 49h 76a 80a 85b 88i 89a			4	21	3			24	52
? Sciomyzidae	—	not considered in the key				7					7
Sepsidae	29	<i>Protorygma electricum</i> Hennig, 1965	1			3					4
familiae inc. sed.	→	sp. 1 & sp. 2: couplets 19h and 40f				2					2
familiae inc. sed.		many different couplets, some without couplets	0	8	3	48	3	0	0	141	203
Sum of included Acalyptratae (at least 217 species: 56 valid taxa, 161 new species)			124	24	57	465	86	13	2	491	1262