A phylogenetic analysis of the subfamilies of Anyphaenidae
(Arachnida, Araneae)

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Introduction

This paper had its origin after I started the revision of the anyphaenid genera bearing a ventral membranous area in the male tegular base. Platnick (1977), who first noted this character, suggested that this group (including the Gondwanan Amaurobioides O. P.-Cambridge, and most of the species assigned to the Neotropical genera Gayenina Nicolet, Oxysoma Nicolet and Tomopisthes Simon), probably deserved subfamily status. Kochalka, in an unpublished thesis (1980), agreed with him and used for the group the name Amaurobioidinae, an available family-rank name after Hickman’s (1949) Amaurobioididae. The name was still used by Lehtinen (1967) in Miturgidae, where he provisionally placed Amaurobioides. Kochalka (1980) presented a partial generic revision of the amaurobioidines, and proposed characters for two monophyletic groups of genera, one related to Amaurobioides, the other to Gayenina. As a phylogenetic framework of the family was needed for a revision of the amaurobioidines, and continued reference or correction of an unpublished work is inconvenient, I decided to continue Kochalka’s effort here.

Materials and methods

Tracheae were examined after digestion of non-cuticular tissues with KOH 10-20% solution at 100°C in a double boiler. Photographs of the tracheal system were made in 75% ethanol. The preparation of spinnerets for SEM study followed Coddington (1989), except that these were air dried. Dissections for muscle observations were made on alcohol-fixed specimens; tissues and organs were removed with fine needles, alternating with ca. 5 seconds of sonication. Postembryonic stages are numbered according to Galiano (1991). All measurements are given in millimeters. See ‘Acknowledgments’ for acronyms of institutions.
The abbreviations of morphological terms used in the text and figures are:

IstB = first bifurcation of median tracheae.
3rdDV = third dorso-ventral abdominal muscle.
3rdPO = third posterior oblique abdominal muscle.
3rdVL = third ventral longitudinal abdominal muscle.
4thAO = fourth anterior oblique abdominal muscle.
4thVL = fourth ventral longitudinal abdominal muscle.
Ac = aciniform gland spigot.
ALE = anterior lateral eye.
ALS = anterior lateral spinneret.
AME = anterior median eye.
ASC = amaurobioidine secondary conductor.
C = conductor.
CD = copulatory duct.
Col = colulus.
CO = copulatory opening.
DP = "dictynoid" pore.
E = embolus.
EB = embolar base.
FD = fertilization duct.
GrC = groove of the conductor.
GrASC = groove of the amaurobioidine secondary conductor.
LTr = lateral tracheae.
MA = median apophysis.
MAmp = minor ampullate gland spigot.
MAMP = major ampullate gland spigot.
MH = median hematodocha.
MTr = median tracheae.
Nu = nubbin of major ampullate gland spigot.
Pi = piriform gland spigot.
PLE = posterior lateral eye.
PLS = posterior lateral spinneret.
PLSp = pulmonar spiracle.
APmA = amaurobioidine paramedian apophysis.
PME = posterior median eye.
PMS = posterior median spinneret.
RTA = retrolateral tibial apophysis.
Sp = spermatheca.
St = subtegulum.
T = tegulum.
TrSp = tracheal spiracle.

Background

The family Anyphaenidae has traditionally included two-clawed spiders with the tracheal spiracle conspicuously separated from the spinnerets. As nearly all spiders known to possess these characters were included in Anyphaenidae, the naturalness of the group was not questioned. The only exception involved the genus Amaurobioides for which Hickman (1949) proposed a separate family, later synonymized with Anyphaenidae (Platnick 1974). In contrast, the rank and superfamilial placement of anyphaenids have remained matters of controversy.

After studying the tracheal system of spiders, Bertkau (1878) proposed the family Anyphaenidae because of the complex tracheal system of Anyphaena Sundevall. At that time, and through the following decades, some large families were recognized on what we today consider as synapomorph criteria. These dump-families, as some authors have termed them, were found on closer examination to be polyphyletic groups whose components could not be placed in well defined families. Good examples of dump-families are the amaurobiids, agelelnids and clubionids. The latter family contained most of the two-clawed spiders with unmodified eyes and spinnerets. Considering that Simon (1897) included in Clubionidae groups as disparate as ctenids and heteropodids, it is understandable that the differences in the tracheal system were overlooked, and that the Anyphaenidae were abandoned as a separate family.

The placement of anyphaenids in a separate family seemed natural after the dissociation of major groups of clubionids into several families. The most comprehensive works on anyphaenids (Platnick 1974; Platnick & Lau 1975) devoted much space to justify the distinction of anyphaenids from clubionids. These authors also provided synapomorphies in support of the monophyly of anyphaenids, primarily from the tracheal system and the claw-tuft hairs.

Interfamilial relationships. – Outgroup relationships of the anyphaenids are far from understood. Basically, two alternative hypotheses have been proposed, each supported by different and conflicting character systems. These assign anyphaenids to a dictynoid and the dionychan lineage, respectively.

Forster (1970) included the anyphaenids in his Dictynoidea, defined by branched median tracheae. He did not explain, however, why other two-clawed spider families with branched median tracheae, such as salticids, thomisids or philodromids, were not included in the Dictynoidea. Kochalka (1980) accepted Forster's view, and proposed a sister group relationship between Notomatachia Forster (Desinae) and Anyphaenidae, based on the median tracheae supplying tracheoles to the prosoma, the protruded chelicerae, the elongate body and the tip of the male palpal cymbium being relatively short. All these characters occur in some anyphaenids, but the association with Notomatachia is untenable. Male
and female genitalia are almost identical in Notomatachia and other desine genera such as Matachia Dalmas, Goyenia Forster and Panon Forster (all figured by Forster 1970), and the characters invoked by Kochalka do not appear to be part of the groundplan of all these genera, but rather autapomorphies of Notomatachia. Furthermore, the protruded chelicerae and elongate body form are not groundplan characters of anyphaenids, but autapomorphies of some genera (e.g., Osoriella Mello-Leitão and Acanthoceto Mello-Leitão).

Bennet (1992) proposed the secondary pores of the spermathecae as a further synapomorphy for dictynoids, but they were not found in dictynines. The discovery of this kind of pores in anyphaenids (Fig. 34; Ramírez, in prep.) might reinforce the hypothesis of a dictynoid lineage. Neverthe-
less, the distribution of this striking character is poorly known, and the pores are also reported from the dionychan families Salticidae (Galiano 1995: fig. 32) and Gnaphosidae (Miller 1967: "Porenkrater" in Zelotes Gistel), as well as in Tegenaria Latreille (Bennet 1992), suggesting a wider distribution than merely Dictynoidea.

The hypothesis that anyphaenids are a dionychan lineage was proposed by Penniman, in his Ph.D. thesis (1985). This author proposed to group Anyphaenidae, Clubionidae, Gnaphosidae, Liocranidae and Corinnidae by the presence of precoxal triangles ("sclerotized triangular extensions of the lateral sternal margins pointing to the coxae"). This hypothesis would be strengthened by the compatible association of Anyphaenidae, Clubionidae and Salticidae by the secondary loss of cylindrical glands (Coddington & Levi 1991).

Notwithstanding, some dictynoid families bear the characters posed to support the dionychan relationship of anyphaenids. At least some hahnids also possess precoxal triangles (Penniman 1985); cylindrical gland spigots are further absent in cybaeids (Bennet 1991: figs 9, 10), and probably dictynids (Kovoor 1987; but see also Coddington 1990 and Platnick et al. 1991).

A third but weak hypothesis of familial relationships of anyphaenids was proposed by Lehtinen (1967: 214), viz., as derivatives of Macrobuninae (Amaurobiidae). This author stated that "the lack of a secondary conductor is obviously primary" in anyphaenids (p. 384), but he reported this structure for Macrobuninae (p. 322). Platnick (1974) argued against a close relationship with macrobunines; he examined the tracheal system of Arctobius Lehtinen, finding a primitive four-
branched pattern. However, *Macrobunus* Tullgren as well as the closely related genera *Rubrius* Simon and *Emmenomma* Simon all have branched median tracheae limited to the abdomen (pers. obs.). This finding makes the placement of *Arctobius* in *Macrobuninae* questionable, and thus Platnick’s finding may not affect Lehtinen’s proposal. The branched median tracheae of *Macrobunus* and its relatives also suggests that they should be added to Dictynoidea sensu Forster, and discussion of Lehtinen’s proposal is addressed below under Dictynoidea. Lehtinen (1967: 384) also suggested relationships of anyphaenids with clubionids and sparassids, but no characters were invoked.

The inclusion of anyphaenids in Forster’s Dictynoidea would at least imply convergence in the loss of the pretarsal claw in anyphaenids and dionychans. Alternatively, inclusion of anyphaenids in Dionycha does not necessarily imply a further convergence in branched median tracheae, because that convergence is assumed to occur, at least, in salticids. The problem of familial relationships of Anyphaenidae is not so much whether the family is included in Dionycha or Dictynoidea, but the actual monophyly those groups. A realistic solution of family relationships will probably require a simultaneous analysis of all families involved, including the vast “amaurobiodeans”. That is obviously beyond the scope of this paper.

**Intraspecific relationships.** – Simon (1897) divided Anyphaenidae in two sections. The section “A”, with two retromarginal teeth and a posteriorly situated spiracle, corresponds broadly with Amaurobioidinae as proposed by Kochalka (1980) and here. Simon’s section “B”, with four or more retromarginal cheliceral teeth and an advanced spiracle, also corresponds broadly with Anyphaeninae as proposed by Kochalka and here. The groups proposed by Simon differ from the present proposal only by the placement of *Coptoprepes* Simon (see below).

Platnick (1977) provided an undisputed synapomorphy linking all amaurobioidines. He stated that “most of the species which have been assigned to the genera *Gayenna*, *Tomopisthes*, *Oxysoma*, *Amaurobioides*, and perhaps others, form a monophyletic group that probably deserves subfamilial status and can be distinguished by the presence of two or three teeth (rather than several small denticles) on the cheliceral retromargin and by a characteristic lightly sclerotized area situated at the proximal end of the male palpal tegulum”. As will be shown in the cladistic section, the membranose area is a synapomorphy of Amaurobioidinae, but the cheliceral teeth are not.

Kochalka (1980) proposed the composition of Amaurobioidinae presented here. He also proposed two groups of genera. The *Amaurobioides* group, with a long and thin male retrolateral tibial
apophysis (RTA), includes Amaurobioides, Axyracrus Simon and Aysenia Tullgren. Kochalka excluded from this group those genera bearing also copulatory ducts wrapped around a longitudinal axis, as in Josa Keyserling. These two characters are in conflict, because the genera Ferrierra Tullgren (Kochalka 1980) and Acanthoceto (Ramírez, in prep.) bear both a thin (but short) RTA and wrapped copulatory ducts.

The second and larger of Kochalka’s groups is the Gayenna – Oxsoma group, with RTA absent and female copulatory ducts thin, leading to distinct, spherical spermathecae (Figs 32, 33). It includes Gayenna, Oxsoma, Tomopistrhes, Aarachosia O. P.-Cambridge, Sanogasta Mello-Leitão, Liparotoma Simon, Philisca Simon, Aporatea Simon, Tasata Simon and Monapia Simon.

The composition of Anyphaeninae adopted here is the same as proposed by Kochalka (1980), with some subsequent additions. No relationships were proposed to date among the genera included. As will be shown below, the monophyly of anyphaenines is supported by the rather weak evidence of three homoplasic characters associated with the advanced tracheal spiracle.

**Taxa examined**

Genera were basically selected in order to test the monophyly of the proposed subfamilies. Some of them were deliberately chosen to disclose the homoplasy of characters. Genera were not selected to resolve phylogenetic relationships inside the subfamily, but only to make explicit the characters and groups proposed by Kochalka (1980).

Subfamilial placements of those genera not included in the matrix were made after examination of the type species, whenever possible. The type species of all amaurobioidine and most anyphaenine genera were examined. Three anyphaenine genera (Lepajen Brescovit, Thaloe Brescovit and Walfilopsis Soares & Camargo) were not available for study, and their placement was decided on the basis of characters taken from the original descriptions.

Data and collections for specimens used in this study are as follows:

*Acanthoceto* sp.: males and females from Argentina, Chubut, Parque Nacional Los Alerces, Lago Futalafquen, Bahía Rosales, 7-II-86, M. Ramírez (MACN); females, third and fourth instar juveniles from Chile, Reg. X, Chiloé, Isla de Chiloé, 15 km S de Chepu, 3-II-91, M. Ramírez (MACN).
*Amaurobioides maritimus* Cambridge, 1883: male and female from New Zealand, Otago, St. Clair Beach, 28-IV-79, J. Carico (OM).
*Anyphaena accentuata* (Walckenaer, 1802): male and female from Belgium, Brussels, IV-1987, M. Ramírez (MACN).
*Arachosia* sp.: male from Argentina, Entre Ríos, Parque Nacional El Palmar, 14-X-91, M. Ramírez (MACN).
*Arachosia* sp.: female from Argentina, Buenos Aires, Punta Lara, 13-IX-81, P. Goloboff, A. Zanetic & M. Ramírez (MACN).
*Axyracrus elegans* Simon, 1884: male and female from Argentina, Tierra del Fuego, Bahía San Antonio, Isla de los Estados, 6-13-II-82, J. Chévez (MACN).
*Aysenia elongata* Tullgren, 1902: female and juvenile syntypes from Chile, Aisén valley, 1-1897, P. Dusén (NRS).
*Aysenia* sp.: male and female from Chile, Reg. VII, Bío Bío, El Manzano, near Contulmo, 3-5-III-86, L. E. Peña (AMNH).
*Aysena prospera* Mello-Leitão, 1944: female from Argentina, Corrientes, Manantiales, no data and collector (MACN).
*Aysena prospera* Keyserling, 1891: male and female from Argentina, Buenos Aires, Hudson, 1-V-84, M. Ramírez (MACN).
*Coptoprepes flavipilosus* Simon, 1884: female from Argentina, Chubut, Parque Nacional Los Alerces, Río Arrayanes, II-85, M. Ramírez (MACN); male holotype from Chile, Cabo de Hornos (MNHN).
*Ferrierra echinata* Tullgren, 1902: females and juvenile syntypes from Chile, Reg. XII, Magallanes, Río Tres Pasos (NRS).
*Gayenna americana* Nicolet, 1849: male and female from Chile, Reg. IX, Malleco, Monumento Natural Contulmo, 12-I-89, M. Ramírez, (MACN).
*Gayenna saccata* Tullgren, 1902: females from Chile, Reg. X, Llanquihue, Caleta La Arena, 30-I-91, M. Ramírez (MACN).
*Lygronoma simoni* Berland, 1913: female from Ecuador, Pichincha, Valle Los Chillos, 29-IV-82, A. Roig (MACN).
*Monapia* sp. female from Argentina: Chubut, Parque Nacional Los Alerces, Lago Verde, II-85, M. Ramírez (MACN).
*Sanogasta intermedia* Mello-Leitão, 1941: female holotype from Argentina, Catamarca, Sanogasta (MLP).
*Sanogasta* sp.: female from Argentina, Buenos Aires, Isla Martín García, 25-V-90, M. Ramírez (MACN); third and fourth instars from Argentina, Buenos Aires, Ingeniero Maschwitz, 12-VII-65, M. E. Galia-no (MACN).
*Sanogasta* sp.: female from Chile, Archipiélago Juan Fernández, Isla Masatierra, 2-I-17, K. Bäckström (NRS).
*Tasata parcepunctata* Simon, 1903: male and female from Argentina, Buenos Aires, Isla Martín García,
Figs 15-20. Female hind tarsal tip: (15-18) *Tomopistes varius*; (15) tarsal tip partially shaved to expose claw tufts; (16) detail of claw tuft; (17) detail of claw tuft setae, external side; (18) detail of claw tuft setae, showing differences in external and internal surfaces; (19) *Ferrieria echinata* Tullgren, tarsal tip; (20) *Malenella nana* sp. n., claw tuft setae.

25-V-90, M. Ramirez (MACN).

*Teudis procerus* Keyserling, 1891: males and females from Argentina, Misiones, Parque Nacional Iguazu, IX-89, M. Ramirez (MACN).


*Teudis cordobensis* Mello-Leitão, 1941: female from Argentina, Córdoba, Alta Gracia, I-81, A. Zanetic & P. Goloboff (MACN).
**Tomopisthes varius** Simon, 1884: male and female from Argentina, Chubut, Parque Nacional Los Alerces, Lago Futalaufquen, II-86, M. Ramírez (MACN).

**Tomopisthes immanis** Simon, 1884: male and female from Argentina, Chubut, Parque Nacional Los Alerces, Lago Futalaufquen, II-86, M. Ramírez (MACN).


**Phylogenetics**

Given the fact that the anyphaenids cannot presently be placed in a reasonably resolved phylogenetic context makes any cladistic analysis of the family somewhat ambiguous, because the optimization of characters used to resolve intrafamilial relationships to some extent depends on the choice of outgroup taxa. In this approach the characters scored for the outgroup do not refer to a particular taxon, but instead to a some sort of consensus of the characters for all potentially related groups, i.e., dionychans and dictynoids. This strategy entails that several entries are scored as variables in the outgroup, and some probably valuable characters are ambiguously optimized (i.e. char. 1 and 15). The advantage is that, on current knowledge, the phylogenetic hypothesis does not depend on unconfirmed hypothesis of relationships.

**Character 1:** position of tracheal spiracle. 0 = posteriorly situated, close to spinnerets. In most potential outgroups the tracheal spiracle is contiguous to the membranose rim at the base of spinnerets. **All dionychans** other than anyphaenids and most dictynoids present this primitive condition. Among dictynoids, the argyronetids and bahnids have the tracheal spiracle in a variably advanced position. The character is coded as variable for the outgroup. 1 = separated from spinnerets, up to halfway to epigastric furrow; in most amauroidiines and **Malenella.** 2 = well advanced, closer to the epigastric furrow; in anyphaenids and **Arachosia** (Amaurobioidinae). The character is considered additive, as there is a clear transition in the position of the tracheal spiracle.

**Character 2:** anyphaenid tracheal pattern (Figs 1-3); see also diagnosis of Amaurobiidae below. 0 = absent. The regular tracheal pattern of anyphaenids is absent in potential outgroups. Very similar patterns are found in distantly related groups as **Prodidomus** Hentz (Lamy 1902: figs 26, 27) and **Uloboridinae** (Uloborus Latreille, Miagrammopes O. P.-Cambridge; Opell 1979: figs 7, 11). Outgroup is scored as O. 1 = present.

**Character 3:** length of lateral tracheae. The length of the posteriorly directed lateral tracheae of anyphaenids appears to be associated with the advancement of the spiracle, because the lateral tracheae always extend to the spinnerets. The character is non-applicable to the outgroup, because potential outgroups (dictynids, bahnids) have no lateral tracheae or have non-comparable structures (lateral tracheae anteriorly directed in dionychans). 0 = short branches; in **Malenella** (Fig. 1) and most amauroidiines (Figs 3, 75). 1 = long branches; in anyphaenids (Fig. 2) and **Arachosia** (Fig. 5).

**Character 4:** position of first thick lateral bifurcation of median tracheae. This character is inapplicable to outgroups. 0 = separated from origin of lateral tracheae (Figs 1, 3, 4, 10, 11, 75); in **Malenella** and amauroidiines except **Arachosia.** 1 = contiguous to origin of lateral tracheae (Figs 2, 6-9); in taxa with far advanced spiracle: anyphaenids and **Arachosia.**

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**Figs 21-23.** Female hind tarsal tip, apical view: (21) **Tomopisthes varius** (Amaurobioidinae); (22) **Ferrieria echinata** (Amaurobioidinae); (23) **Malenella nana** sp. n. (Malenellinae).
**Character 5:** claw tuft hairs. $0 =$ moderately flattened setae. There is wide diversity in the structure of claw tuft setae, probably reflecting independent origins of claw tufts. Some dionychans have spatulate setae, as the prodidomid *Lygromma* Simon (pers. obs.) and the liocranid *Scotinella* Banks (Platnick & Lau 1975: fig. 19), but they appear to have arisen in derived branches of those families. Accordingly, the character is coded 0 for outgroup. $1 =$ spatulate setae; anyphaenids have characteristic broadly flattened setae (Figs 15-23; Platnick & Lau 1975: figs 11-14).

**Character 6:** orientation of claw tuft setae. $0 =$ flat sides up- and downwards; this is the generalized condition in dionychans (Platnick & Lau 1975), and *Malenella* (Fig. 23). $1 =$ ridged side directed outwards (Platnick & Lau 1975); a synapomorphy for anyphaenines plus amaurobioidines (Figs 21, 22). At least *Lygromma* (pers. obs.) and *Scotinella* (Platnick & Lau 1975: fig. 19) appear to have attained this state through convergence.

**Character 7:** number of retromarginal cheliceral teeth. Highly variable through outgroups. $0 = $ two; in most genera of the Gayenna-Oxyoma group less *Philisca*, *Tasata*, and some disparate species (*Liparotoma trypunctatum*; Ramirez 1993); also in most species of *Josa*. $1 = $ three; at least in *Amaurobioides* and *Philisca*. $2 = $ four or more; in all anyphaenines and *Malenella*; some amaurobioidines have a series of small denticles, e.g., *Coptoprepes* and *Ferrieria*. The character is considered non-additive.
Character 8: thickened female palp. 0 = absent. 1 = present (Fig. 67), an autapomorphy of Malenella.

Character 9: patch of blunt hairs on female palpal tarsi. 0 = absent. 1 = present (Figs 67, 68), an autapomorphy of Malenella.

Character 10: AME much smaller than ALE. This character is scored to test a possible association between Malenella and Wulfila O. P.-Cambridge. 0 = absent, in most potential outgroups. 1 = present, in Malenella (Fig. 63) and Wulfila.

Character 11: number of tibial apophyses. 0 = one. One retrolateral tibial apophysis appears to be the common pattern in entelegynes, but number and shape are highly variable in potential outgroups. Some amaurobioidines have this condition, as well as some unscored anyphaenines. 1 = two or more; in Malenella and most anyphaenines there is a complex system of tibial apophyses. 2 = none; in the Gayenna-Oxysoma group there is no male tibial apophysis, as well as in the genus Josa (Kochalka 1980). The character is considered non-additive.

Character 12: spine-like retrolateral tibial apophysis. 0 = absent. 1 = present (Forster 1970: fig. 470). This is a potential synapomorphy linking some genera probably related to Amaurobioides, as Aysenia, Axyracrus, Ferrieria and Acanthoceto. In this analysis, the character is ambiguously optimized in all three dichotomous resolutions. Ambiguity is caused by the missing entries for the Gayenna-Oxysoma group which lacks the tibial apophysis, and by the presence of a spine-like apophysis in some Coptoprepes.

Character 13: sclerotized, often protruding, grooved cymbial tip. 0 = absent; in outgroup and Malenella. Salticids often have a wide superficial groove in the cymbial tip where the embolus rests, but it is weakly sclerotized and not protruding. 1 = present (Figs 26, 29). Coddington (1990) suggested that the cymbial tip could have the function of a conductor. This is a putative synapomorphy of anyphaenines plus amaurobioidines.

Character 14: tegulum with a deep notch occupied by the median haematodocha, visible as a membranose area in the tegular proximal end (Platnick 1977; Ramírez 1993). 0 = absent; the tegulum has a regular posterior outline without notch (e.g. Brescovit 1992b: figs 8, 9). 1 = present (Figs 26-28). This is an unambiguous synapomorphy of anyphaenines.

Character 15: presence of median apophysis. 0 = present. The median apophysis appears to be part of the groundplan of the enteleyn male palp (Coddington 1990). In anyphaenines and amaurobioidines the
Figs 32-34. Female genitalia of Gayenna-Oxysoma group: (32) Gayenna americana, ventral view; (33) Gayenna sacculata Tullgren, dorsal view; (34) Monapia sp., detail of spermathecal base, showing the "dictynoid" pore. CD = copulatory duct; CO = copulatory opening; DP = "dictynoid" pore; FD = fertilization duct; Sp = spermatheca.

median apophysis is present in a rather unmodified condition. 1 = absent; in Malenella (Fig. 65). Notably, the median apophysis is absent in many potential outgroups, such as dictynids and related families (Argyrozetidae, Cybaeidae), most hahniids (Forster 1970) and corinnids (Penniman 1985; Ramírez et al., in press). Scored as variable for outgroup.

Character 16: shape of median apophysis. 0 = moderately thick. It appears to be the basic state of entelegynes. 1 = slender (Figs 29-31); a putative synapomorphy of the Gayenna-Oxysoma group.

Character 17: grooved conductor. 0 = absent; in the Gayenna-Oxysoma group, the conductor is apparently absent, and its function accomplished by the amauroidioidine secondary conductor. 1 = present. The embolus runs through a groove of the conductor in some amauroidioidines (Figs 27, 28) related to Coptoprepes and Amaurobioides. The condition is also present in several potential outgroups, such as dictynids and related families (Bennett 1991). Scored as variable in outgroup.

Character 18: shape of "amaurobioidine paramedian apophysis" (APmA; "paramedian apophysis" of Ramírez 1993). Homology of this sclerite of the amauroidioidine palp with similar sclerites in either anyphaenines or other families is uncertain. The terminology seems proper on descriptive grounds, but a taxon reference is added to avoid a dubious statement of homology. 0 = thick, not closely associated with median apophysis (Fig. 29). 1 = thin, closely associated with median apophysis (Figs 30, 31); a synapomorphy linking at least Sanogasta Mello-Leitão and Arachosia.

Character 19: female copulatory ducts thin, leading to distinct, spherical spermathecae (Kochlka 1980; Ramírez 1993). 0 = absent. 1 = present (Figs 32, 33). A synapomorphy of the Gayenna-Oxysoma group. A few anyphaenines like Istigonia Simon (Brescovit 1991) have a similar pattern, but the ducts are notably short.

Character 20: presence of amauroidioidine secondary conductor. 0 = absent. 1 = present. A synapomorphy of Amaurobioidinae. This sclerite is often associated with the conductor, and also possesses a groove where the embolus rests (Fig. 29). The groove is reduced but recognizable in genera such as Tomopistes and Liparotoma.

The data matrix of Table 1 was analyzed with parsimony programs under equal weights to produce an exact solution using Hennig86, version 1.5 (Farris 1988) and Nona version 1.15 (Goloboff 1994b). For the analysis with Hennig86 polymorphies were coded as missing entries, because polymorphic taxa comprise the entire range of the character in all cases. The exact solution (command ie:) produced two trees of length = 26, the consensus of which is shown in Fig. 35. The first tree was identical to the consensus, the second placed Coptoprepes as the sister group of Amaurobioides + Ferrieria. The exact solution of Nona (command mswap+) produced the same cladogram as in Fig. 35, ignoring potential support due to ambiguous optimizations of characters (option ambiguous-:). Note that although polymorphic characters are transformed to ranges when consid-

Table 1. Data matrix for sampled genera of Anyphaenidae; $x = [0, 1]$; $y = [0, 1, 2]$.

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<th>outgroup</th>
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<th>Wulfitla</th>
<th>Anyphaena</th>
<th>Coptoprepes</th>
<th>Amaurobioides</th>
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Fig. 35. Most parsimonious cladogram for sampled genera of Anyphaenidae. Character state changes noted on branches.

Discussion

The present analysis indicates that Anyphaenidae is a monophyletic group supported by two characters, the pattern of the tracheal system (char. 2) and the spatulate setae of claw tufts (char. 5). The advancement of the tracheal spiracle would be a synapomorphy of the family only if it is shown to be related to spiders with a posteriorly situated spiracle.

The first dichotomy places Malenella as the sister group of all other anyphaenids. The thickened tarsi and patch of blunt hairs on the female palp (char. 8 and 9) are undisputed autapomorphies of Malenella, while the small median eyes (char. 10) appear independently developed in Wulfila. Anyphaenines and amaurobioidines are sister groups united by the orientation of claw tuft setae, with ridged sides directed outwards (char. 6), and by the grooved cymbial tip (char. 13).

The monophyly of Anyphaeninae is supported by the advancement of the tracheal spiracle to near the epigastric furrow (char. 1 state 2), plus two related characters: the lateral tracheae have long branches reaching the spinnerets (char. 3), and the first thick lateral bifurcation of median tracheae is contiguous with the origin of the lateral tracheae (char. 4). All three characters are homoplasic, reappearing in Arachosia, an amaurobioidine genus with a rather forwardly advanced spiracle.

The monophyly of Amaurobioidinae is supported by two synapomorphies. The ingression of the median hematodocha in the tegulum (char. 14) is a complex and undisputed synapomorphy. The amaurobioidine secondary conductor (char. 20) is another synapomorphic state of the male palp of amaurobioidines. Note that state 2 of char. 7, four or more retromarginal cheliceral teeth, optimizes at the base of Amaurobioidinae, in conflict with...
Platnick (1977, see above). However, inclusion of other taxa like Philisca (with 3 teeth), Josa (with 2 teeth) and Acanthoceto (with 2 to 5 teeth) is needed to seriously test his hypothesis.

Two groups are recognized among amaurobioidines. The genera related to Amaurobioides are united by the presence of a conspicuous, grooved conductor (char. 17). The Gayenna-Oxysoma group is defined by having the female copulatory ducts thin, leading to distinct, spherical spermathecae (char. 19), the thin and sigmoid median apophysis (char. 16), and the two retromarginal cheliceral teeth (char. 7). The genus Arachosia is atypical among amaurobioidines in that some species have the tracheal spiracle closer to the epigastric furrow than to the spinnerets. Nevertheless, its position in amaurobioidinae is strongly supported by the evidence of char. 13, 14, 16-19. Arachosia is grouped with Sanogasta by the thin amaurobioidine paramedian apophysis closely associated with the median apophysis (char. 18).

Most authors homologize the inner lateral trunks of complex tracheal systems with the lateral tracheae found in simple four-branched systems. As noted by Forster (1970), some members of his Dictynoidea have no traces of lateral tracheae, as in some Dictynidae (his figs 21 and 22), Myronininae (fig. 13), Toxopinae (fig. 10 and 11) and probably Hahniidae (fig. 19 and p. 140). When trying to find support for the inclusion of Anyphaenidae in Dictynoidea, the question arose of whether the basal lateral trunks of anyphaenids are homologous with the lateral tracheae or with branches of the median trunks, i.e., whether lateral tracheae are present or not. The same question would also apply to the lateral tracheal bunches of argyronetids. Some developmental observations may render a preliminary answer to this question. Dissections of third instar Amaurobioides sp. showed a simple four-branched tracheal system (Figs 70, 71), with tiny lateral tracheae, and median tracheae limited to the abdomen. Second and third instars of Sanogasta sp. and Acanthoceto sp. have a similar pattern, with hardly visible lateral tracheae (Fig. 73), transforming in the fourth instar to a fully developed tracheal system (Fig. 74), almost identical to the pattern found in adults (Fig. 75). As lateral tracheae are present in juveniles, it seems reasonable to homologize them with the basal lateral trunks found in fourth and subsequent instars. The anyphaenines have basal lateral trunks arising from two main stems at each side of the spiracle (Figs 2, 6-9). The most basal ones are straight, caudally directed, and appear to be homologous with lateral tracheae. The following branches are laterally directed, and appear to be homologous with the first thick lateral bifurcation of median tracheae observed in amaurobioidines (Fig. 3) and malenellines (Fig. 1). This hypothesis of homology is also supported by muscle positions. The third dorsoventral muscle unites with longitudinal and oblique muscles just dorso-anteriorly to the first bifurcation of the median tracheae (Fig. 13), and the 3rd posterior oblique muscle splits in several branches just anterior to this bifurcation. In anyphaenines (Fig. 14) the tracheal tubes are displaced forward by the forward advancement of the spiracle, but the 3rd dorsoventral and oblique muscles remain in their original positions. As the first median bifurcation retains its posterior position relative to the 3rd posterior oblique muscle, they are adjacent to the advanced lateral tracheae.

In his unexcelled work on spider tracheae, Lamy (1902: figs 26, 27) illustrated the tracheal system of Prodidomus amaranthius Lucas, showing a pattern strikingly similar to that found in anyphaenids. As there are many characters supporting the inclusion of Prodidomus in Gnaphosoida (Platnick 1990), and another prodidomid genus examined (Lygromma, pers. obs.) exhibited the simple four-branched tracheal system of gnaphosids (Lamy 1902: fig. 28), the tracheal pattern of Anyphaenidae and Prodidomus supposedly arose through convergence. A very similar tracheal pattern is also present in the uloborid genera Uloborus and Miagrammopes (Opell 1979: figs 7, 11), but it is for other reasons highly unlikely, that these taxa are closely related to anyphaenids.

**Proposed classification**

Family ANYPHAENIDAE Bertkau


**Diagnosis.** – Two-clawed spiders with paired claw-tufts, each composed of 2-8 rows of spatulate hairs. Tracheal system presents a broad spiracle separated from the spinnerets, and a character-
istic pattern of tracheae (Figs 1-11): lateral trunks moderately thick, branching adjacent to spiracle and with all branches limited to abdomen; median trunks thick, giving off tracheoles and minor branches at intervals in the abdomen, and near the pedicel splitting into several minor trunks extending to the legs and cephalic area.

Description. – Small to large (2.5-22 mm) spiders. Eight eyes in two rows, secondary eyes with
canoe-shaped tapetum. Median ocular area longer than wide. Labium not fused with sternum, endites with interior margins subparallel, with serrula and scopula. Precoxal triangles usually present. Chelicerae free, with boss. Abdomen oval, one pair of book lungs and complex tracheal system, tracheal tubules lined with spiculae coalescing in spiral thread (Fig. 12); without cribellum and calamistrum. Two or three pairs of cardiac ostia. Six spinnerets, ALS subconical, contiguous, with short terminal segment bearing two major ampullate gland spigots (Figs 36, 42), the posterior usually reduced to a nubbin (Figs 39, 45, 48), and several piriform gland spigots. PMS cylindrical, slightly smaller than anteriors, with two (Figs 37, 40, 46), one (Fig. 49), or no (Fig. 41) minor ampullate gland spigots and several aciniform gland spigots usually with long bases (Figs 38, 41, 47, 50), cylindrical gland spigots absent. PLS cylindrical, slightly longer than anteriors, terminal segment usually hemispherical or conical, as in Macrophyses O. P.-Cambridge and Anyphaenoides Berland (Brescovit 1992a, c), with several aciniform gland spigots, usually with long bases (Figs 38, 41, 47, 50), cylindrical gland spigots absent. Colulus reduced to patch of hairs, paired in third instar juveniles (Fig. 72). Genitalia entelegyne, spermathecae with secondary “dictynoid” pores (at least in amaurobioidines, Fig. 34), male palp with RTA (reduced or absent in some amaurobioidines), cymbium with concave projecting tip (except in Malenella), bulb with median apophysis usually hooked (absent in Malenella), subtubegonium exposed on prolateral side. Legs prograde, anterior metatarsi and all tarsi scopulate, tarsi with two pectinate claws and claw-tufts, composed of two (Fig. 23) to eight (Fig. 25) rows of spatulate setae on each side. Trichobothrial bases with parallel longitudinal ridges (Figs 54-57), tarsal organ capstrate, with ovoid (Fig. 51) or elongate aperture (Figs 52, 53). Eggs grouped inside retreat by sparse threads of silk (Simon 1897: 96), without dense eggsac (probably correlated with absence of cylindrical glands).

Subfamilies included. – Malenellinae, Anyphaeniinae and Amaurobioidinae.

Taxonomic remarks. – Platnick (1974) proposed the alignment of claw tuft setae in two rows on each side as a synapomorphy for anyphaenids. At least some amaurobioidines have setae in up to eight rows. The number of rows and setae per row appears related to body size, as suggested by comparing the largest (Figs 24, 25) and smallest (Figs 19, 22) amaurobioidines. The same is true in the course of development. A few tuft setae appear first in the postembryonic fourth instar, with number increasing in subsequent instars (pers. obs.). The sequence is the same in salticids, as described by Hill (1977). The claw lever (Fig. 25) is also similar in salticids and anyphaenids in the arrangement of the slit sensilla (see Hill 1977: pl. 2 A, B), and this arrangement is also seen in at least liocranids (Ubick & Platnick 1991: fig. 3), corinnids (pers. obs.) and the lycosoid genus Machadonia Lehtinen (Griswold 1991: fig. 26). In Tomopistes immanis Simon the claw lever differs from that of salticids in having a median ventral furrow and a subapical small cone that could be a rudimentary third claw, similar to what Griswold (1991: fig. 18) found in Machadonia. Platnick (1974) proposed that sexual dimorphism in the tracheal system was as an additional character for anyphaenids; he stated that male anyphaenids have considerably thicker tracheae than females, basing his observations on Hibana gracilis (Hentz) (under Aysha) and three species of Anyphaena. I did not examine these genera, but my observations in other anyphaenines and amaurobioidines did not support this. Only slight differences between sexes were found, with larger tracheae either in the males (Figs 3, 4 and 10, 11) or the females (Figs 6, 7 and 8, 9). Tracheal thickness appears to be more correlated with abdominal size than with sex; the difference found by Platnick could be a synapomorphy for a less inclusive group in Anyphaeninae.

Kaston (1948), following Petrunkevitch (1933), considered the presence of only two pairs of ostia as an anyphaenid character. The latter author studied the heart of the anyphaenines Anyphaena, Wulftia and Hibana Brescovit (under Aysha tenuis). On the other hand, Hickman (1949) reported three pairs of ostia for Amaurobioides, and Kochalka (1980) reported also three for Hibana velox (Becker) and the amaurobioidines Joana nicoleti (Simon) and Amaurobioides sp. Whether the character is variable or some observations are wrong must await future morphological work.
Subfamily MALENELLINAE subfam. n.

Type genus: Malenella gen. n.

This subfamily currently contains only one genus and species. Diagnosis and description as for species (see below).

Genus Malenella gen. n.

Type species: Malenella nana sp. n.

Etymology. – The name is a diminutive dedicated to my teacher María Elena (Malena) Galindo.

Diagnosis and description as for species (see below).
Fig. 48-53. *Malenella nana* sp. n. (Malenellinae), spinnerets in apical view; (51-53) tarsal organ on hind tarsus: (51) *Ferrieria echinata*; (52) *Tomopistes imminis*; (53) *Malenella nana* sp. n. ALS = anterior lateral spinneret; mAmp = minor ampullate gland spigot; MAmp = major ampullate gland spigot; Nu = nubbin of major ampullate gland spigot; PLS = posterior lateral spinneret; PMS = posterior median spinneret.

**Malenella nana sp. n.**

(Figs 1, 20, 23, 48-50, 53, 56, 57, 58-69)

*Type material.* – Female holotype and male paratype from Chile: Región VIII (Biobío), Concepción Prov., Cerro Caracol, Ciudad de Concepción, 200m, 36°51'S, 73°02'W. 17.XI.1993, N. Platnick, K. Catley, M. Ramírez & T. Allen (AMNH).

*Etymology.* – The specific name refers to the small size of the species.

*Diagnosis.* – Females and small juveniles can be distinguished from those of all other anyphaenids by the thickened palpal tarsi (Fig. 67). Males can...
be recognized by the short, stout embolus and by the absence of a median apophysis (Fig. 65).

**Description.** — Female (holotype): Total length 4. Carapace 1.50 long, 1.23 wide. Length of tibiae/metatarsi: I 1.17/1; II 0.75/0.72; III 0.53/0.67; IV 0.93/0.90. Eyes as in Fig. 58, AME much smaller than other eyes. Chelicerae with 3–4 promarginal and 4 retromarginal (2 basal smaller) teeth. Labium short, apically rounded (Fig. 59). Thoracic groove hardly visible. Palpal tarsi thick, bearing dorsal patch of blunt hairs (Fig. 67, 68). Tracheal spiracle 1/4 distance between spinnerets and epigastric furrow, origin of lateral tracheae slightly advanced from spiracle (Fig. 1). AMS with one major ampullate gland spigot, adjacent nubbin (Fig. 48) and ≈16 piriform gland spigots; PMS with one minor ampullate and ≈7 piriform gland spigots (Fig. 49); PLS with ≈20 piriform gland spigots with elongated bases (Fig. 43). Epigynum with broad central depression and prominent posterior margin (Fig. 61). Internal genitalia with short, thick, curved copulatory ducts, leading to subespherical spermathecae, with internal projections (Fig. 62). Claw tufts composed of curved lamelliform setae, sides directed dorsoventrally (Figs 20, 23), aligned in two rows on each side. Spines: I (Fig. 60): Femur 0-0-1-2. Tibia v 2-2-0, p 1-1. Metatarsus v 2-2-0-0, d 2ap, p and r 1-1. II: Femur = I. Tibia v 1r-1r-0, p 0-1. Metatarsus v 2-2-1, p 1-1, r 0-1, d 2ap. III: Femur = I. Tibia v 1p or 0. Metatarsus v 0-2-1, p 1-1, r 1ap, d 2ap. IV: Femur = I. Tibia v 2ap, r 1ap. Metatarsus v 0-2-1, p, r 1-1, d 2ap. Palp: Femur d 0-0-1-1. Tibia p 2-0, d 1-1. Tarsus p 2bas, r 2-1. Trichobothria in two rows on tibiae, one row on metatarsi and tarsi. Colour light green, fading in alcohol to white or cream.

**Male (paratype):** Total length 3.60. Carapace 1.45 long, 1.08 wide. Length of tibiae/metatarsi: I
Figs 58-62. *Malenella nana* sp. n., female: (58) body, dorsal; (59) ventral; (60) first leg, prolateral; (61) epigynum; (62) cleared vulvae, dorsal. CO = copulatory opening.

1.3/1.08; II 0.98/0.68; III 0.52/0.67; IV 0.88/0.85. Chelicerae longer than in female (Fig. 63). Palp with three retrolateral tibial apophyses (Fig. 66), two almost dorsal and conical, one almost ventral, flattened; cymbium with rounded apex. Embolus short, stout, fused to tegulum, with adjacent hyaline conductor; median apophysis absent (Fig. 65). Spines as in female, but: palpal tibia d 1, cymbium r 0.

Note: The apically unpaired ventral spines on metatarsi II-IV are remarkable among anyphaenids.


Distribution. – Central and southern Chile, regions V through X.

Natural history. – Specimens were collected on foliage of trees 1-2.5 m above the ground.

Subfamily ANYPHAENINAE Bertkau

Diagnosis. – Recognized by the forwardly advanced tracheal spiracle, situated closer to the epigastric furrow than to the spinnerets (Fig. 2). Some amaurobioid species have a rather forwardly advanced spiracle, but they can be distin-
guished by the characteristic membranose tegular area.

**Description.** – Small to medium sized (4-10 mm) spiders. Chelicerae with 4 or more retromarginal teeth. Tip of labium usually notched. Tracheal spiracle midway between epigastric furrow and spinnerets or nearest to furrow. Lateral tracheae well developed, reaching spinnerets (Fig. 2). Male palpal tibia usually with multiple retrolateral apophyses. Cymbial tip concave, closely associated with embolus. Tegulum without membranous basal area; secondary conductor absent. Claw tufts composed of wide spatulate hairs, sparsely ciliated side directed outward or obliquely, 2-4 rows on each side. Trichobothria in single row on metatarsi, two rows on tarsi.

**Comment.** – The anyphaenines correspond broadly with the second section of Anyphaeneae in the key of Simon (1897: 93, 102), characterized by four or more retromarginal cheliceral teeth and advanced spiracle. His grouping differs only by the inclusion of Copioprepes, here placed in Amaurobioidae.

**Genera included.** – Anyphaena Sundevall, 1833; Anyphaenoides Berland, 1913; Australaena Berland, 1942; Aysha Keyserling, 1891; Bromelina Brescovit, 1993; Hibana Brescovit, 1991; Isigonina Simon, 1897; Lepajan Brescovit, 1993; Macrophyses O. P.-Cambridge, 1893; Mesilla Simon, 1903; Osoriella Mello-Leitão, 1922; Patrera Simon, 1903; Sillus F. O. P.-Cambridge, 1900; Tafana Simon, 1903; Temnida Simon, 1897; Teu-
The type species for most included genera were examined, and they all had the characteristic forwardly displaced tracheal spiracle. Type species of three genera were not available for study: Wulfilopsis, which also has a forwardly advanced tracheal spiracle; and Lepajian and Thaioe, as described in detail by Brescovit (1993a, b), both have a forwardly advanced tracheal spiracle, a grooved cymbial tip, and a median apophysis.

**Taxonomic remarks.** – The monophyly of anyphaenines is supported by three char. (1, 3, 4), all pertaining to the spiracle and tracheae. Convergencies are found in Arachosia, an amaurobiodine taxon. The grooved secondary conductor present in amaurobiodinides appears to have no counterpart in anyphaenines. The possible homology of the sclerites articulated to the tegulum in the most complex anyphaenine palps, for instance the “tégular projection” in Thaioe (Brescovit 1993b: figs 4, 6 and 9), remains to be studied.

**Subfamily AMAUROBIOIDINAE Hickman**


**Diagnosis.** – Recognized by the tegulum with a deep notch occupied by part of the median haematodocha, visible as a membranose area in the tegular proximal end (Figs 27-29).

**Description.** – Small to large (2.50-22 mm) spiders. Chelicerae with 2-7 retromarginal teeth, exceptionally one. Tip of labium rounded or very slightly notched. Male palp with single or absent RTA. Cymbial tip short, with ventral concavity closely associated with embolus. Embolus articulated to tegulum, filiform to moderately thick, the tip usually resting in a secondary conductor (Fig. 27, 29). Tracheal spiracle from close to spinnerets to midway between epigastric furrow and spinnerets (except in Arachosia, with spiracle slightly advanced from midpoint, Fig. 5). Lateral tracheae of variable development (the more advanced the spiracle the more lengthened the lateral tracheae; compare Figs 3, 75 with 5). Spermathecae with conspicuous “dictynoid” pores (Fig. 34). Claws tufted composed of 2-8 rows of wide spatulate hairs on each side, with sparsely ciliated sides directed outward or obliquely. Trichobothria in single row on metatarsi, two rows in tarsi.

**Comment.** – The amaurobiodinides correspond broadly with the first section of Anyphaenae in the key of Simon (1897: 90, 97), with two retromarginal teeth and a posteriorly situated spiracle. His grouping differs only by the inclusion (p. 102) of Coptoprepes in his second section.

**Genera included.** – Acanthoceto Mello-Leitão, 1944; Amaurobioides O. P.-Cambridge, 1883; Aporatea Simon, 1897; Arachosia O. Pickard-Cambridge, 1882; Axyracrus Simon, 1884; Ayenia Tullgren, 1902 (here transferred from Clubionidae); Coptoprepes Simon, 1884; Ferrieria Tullgren, 1901; Gayenna Nicolet, 1849; Gayennella Berland, 1913; Josa Keyserling, 1891; Haptisus Simon, 1897; Liparotoma Simon, 1884; Monapia Simon, 1897; Olbophtalmus Simon, 1904; Oxysoma Nicolet, 1849; Philisca Simon, 1884 (here transferred from Miturgidae); Sanogastta Mello-Leitão, 1941 (here transferred from Corinnidae); Tasata Simon, 1903; Terupis Simon, 1904; Tetromma Keyserling, 1877; Tomopistes Simon, 1884.

Several of these generic names will be synonymized after a detailed revision of the subfamily. Type species of all genera were examined; all have the characteristic notch in the tegulum.

**Acknowledgments**

John Kochalka kindly provided a copy of his Ph. D. Thesis, and discussed many problems on anyphaenid systematics. Rob Bennett sent me a copy of his Ph. D. Thesis. Maria Elena Galiano permanently guided and encouraged my study; she also reared and provided many post-embryos for study of tracheal development. Antonio Brescovit provided precious comments on anyphaenid systematics; he also provided SEM pictures of Malenella. Pablo Goloboff arduously read an early draft of the manuscript and proposed many useful changes. Helpful comments on a draft of the manuscript were provided by María Elena Galiano, Charles Griswold, Antonio Brescovit, Norman Platnick and specially Pablo Goloboff. I specially acknowledge the comments of the reviewer, Nikolaj Scharff, who pointed to important blunders in the manuscript. Patricia Sarmiento provided valuable assistance with the SEM work. This project was supported by a graduate fellowship of the Universidad de Buenos Aires.

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Figs 70-75. Postembryonic development of tracheae and colulus; (70-72) *Amaurobioides* cf. *boydi*: (70) third instar, abdomen, ventral; (71) detail of tracheae; (72) paired colulus; (73-75) *Samuza* sp. (Ing. Maschwitz): (73) third instar, detail of tracheae; (74) fourth instar; (75) adult female. 1stB = first bifurcation of median tracheae; Col = colulus; LTr = lateral tracheae; MTr = median tracheae; PlSp = pulmonar spiracle; TrSp = tracheal spiracle.
References


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