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PHYLOGENETIC ANALYSIS OF PISAURINE NURSERY WEB SPIDERS, WITH REVISIONS OF *TETRAGONOPHTHALMA* AND *PERENETHIS* (ARANEAE, LYCOSOIDEA, PISAURIDAE)

Petra Sierwald: Center for Evolutionary and Environmental Biology, Field Museum of Natural History, Chicago, Illinois 60605 USA

ABSTRACT. Apomorphic characters of the Pisaurinae Simon 1898, here recognized as a monophyletic clade comprising 19 nominal pisaurid genera, are described. The genera *Perenethis* L. Koch 1878 and *Tetragonophthalma* Karsch 1878 are revised. Three Asian, two African and one Australian species of the genus *Perenethis* are recognized. The Asian species of the genus *Perenethis* comprise *Ocyala dentifasciata* O. Pickard-Cambridge 1885, *Tetragonophthalma fascigera* Bösenberg & Strand 1906, and *Tetragonophthalma sindica* Simon 1897. A lectotype is designated for the Australian species *Perenethis venusta* L. Koch 1878. *Perenethis parkinsoni* Dahl 1908 is regarded as a subjective junior synonym of *P. venusta*. The African species of *Perenethis* are *Tetragonophthalma simoni* Lessert 1916, and *Tetragonophthalma symmetrica* Lawrence 1927 with its subjective junior synonyms *Perenethis huberti* Blandin 1975, *Perenethis lejeuni* Blandin 1975 and *Pisaurellus badicus* Roewer 1961. A lectotype is here designated for the African species *Perenethis simoni*. *Phalaea vulpina* Simon 1898 is the only recognized species of the genus *Tetragonophthalma* with eight subjective junior synonyms: *Tetragonophthalma balsaci* Blandin 1976, *Phalaea crassa* Thorell 1899, *Phalaea ferox* Pocock 1899, *T. guentheri* Roewer 1955, *T. lecordieri* Blandin 1976, *T. pellengea* Roewer 1955, *Phalaea thomensis* Simon 1909, and *T. wittei* Roewer 1955. *Cispius novus* Caporiacco 1941 and *Cispius tertali* Caporiacco 1941 are both subjective junior synonyms of *Cispius aethiopicus* Caporiacco 1939, now placed in the genus *Charminus* (NEW COMBINATION). The genera *Charminus* Thorell 1899, *Cispius* Simon 1898, *Tetragonophthalma*, *Afropisaura* Blandin 1976, *Perenethis*, *Maypacius* Simon 1898, and *Polyboea* Thorell 1895 form a monophyletic group within the Pisaurinae, here called *Perenethis* genus group. The copulatory organs of this group are figured in detail, the vulval structures for the first time. Males and females of the poorly-known monotypic genus *Polyboea* are described, and their copulatory organs are figured for the first time. A cladistic analysis of the *Perenethis* genus group is presented. The Afro-Asian distribution of members of the clade *Polyboea* and *Maypacius* and the *Perenethis*-clade is hypothesized to be the result of independent range extensions during the expansion of suitable habitats between the Miocene and the beginning of the Pleistocene.

The nursery-web spiders (Family Pisauridae) currently contain 54 nominal genera (Platnick 1993), many of them only poorly known. Members of the family are distributed worldwide, displaying great variations in habitus, size and life style. Several genera contain large species (up to 30 mm body length) hunting on the surface of freshwater ponds and streams, (e.g., members of the worldwide genus *Dolomedes* Latreille 1804 and the African-Asian genus *Thalassius* Simon 1885 (see Sierwald 1987)), or hunt in trees like spiders of the African genus *Tetragonophthalma*. Other genera contain small spiders (body length 3–4 mm) hunting on permanent webs, (e.g., in the American genus *Architis* Simon 1898 (see Carico 1981)). Spiders of the name-bearing Palearctic genus *Pisaura* Simon 1885 hunt in the vegetation. A well-known species is *Pisaura mirabilis* (Clerck 1757), famous for the male's nuptial gift presented to the female during courtship. Morphological data, especially of copulatory organs, life history data and revisionary work at the alpha-taxonomic level, are lacking for most Pisauridae. For many genera, only very few (type) specimens are cataloged and thus accessible in collections. Most American (Carico 1972–1981) and some African (Blandin 1974a–1979b; Sierwald 1987) pisaurid genera were revised recently.

The main systematic problem of this family concerns the delineation of the Pisauridae and the definition of subfamilies. No synapomorphies have been recognized to date that would distinguish at least the majority of pisaurid genera as a single clade. The often cited nursery-web appears not to be restricted to pisaurid genera, but similar (homologous?) webs are constructed by *Peucetia* Thorell 1869 (Family Oxyopidae; Brady 1964; Zahl 1971, color photo of *Peucetia* nursery-web) and *Ancylometes* Bertkau 1880 (see Merrett 1988). The systematic position of the latter is uncertain, as it shares characters with members of the family Ctenidae (eye pattern, reduced third claw), a group that is presumably not monophyletic (Griswold 1993; Huber et al. 1993). Eye arrangements have a long tradition in identification, separation and delimitation of spider taxa at and below the family level. However, the general "pisaurid" pattern (recurved posterior eye row wider than anterior eye row) occurs also at least in the families Trechaleidae, Lycosidae, Psechridae, Ctenidae, Acanthoctenidae, and Senoculidae. Formerly, the pisaurid genera were grouped in the three subfamilies Pisaurinae, Thaumasiinae and Thalassiinae (Simon 1898a; Roewer 1954). Lehtinen's (1967) suggested placement of "pisaurid" genera in different families (Dolomedidae = Thaumasiinae and Pisauridae = Pisaurinae) and superfamilies (Lycosoidea and Pisauroidea) was poorly substantiated, the argumentation lacking supportive evidence in form of clearly defined synapomorphies (Brignoli 1983; Sierwald 1990). New catalogs (Platnick 1989, 1993) listed pisaurid genera without reference to subfamilies.

Recent progress in systematic studies identified 10 genera, originally assigned to Pisaurinae and Thaumasiinae, as a monophyletic clade. Based in part on characters of the eye arrangement and synapomorphies in male and female copulatory organs (Sierwald 1993), these 10 genera were placed in the re-erected South American family Trechaleidae Simon 1890 (Carico 1986, 1993). The present study describes the defining characters of a monophyletic clade consisting of 18 pisaurid genera all related to the genus *Pisaura* and for which Simon's name Pisaurinae is available (Tables 2, 3). This study also presents a cladistic analysis of a monophyletic clade within the here redefined Pisaurinae, the *Perenethis* genus group. This group contains the genera *Charminus* Thorell 1899, *Cispius* Simon 1898, *Afropisaura* Blandin 1976, *Tetragonophthalma* Karsch 1878, *Perenethis* L. Koch 1878, *Maypacius* Simon 1898 and *Polyboea* Thorell 1895. The majority of characters used in the cladistic analysis stem from the copulatory organs and the internal female organs for these taxa are figured for the first time. Taxonomic revisions of the genera *Tetragonophthalma* and *Perenethis* are included. The distribution of members of the *Perenethis* genus group is noteworthy and discussed below. *Charminus*, *Cispius*, *Afropisaura*, *Tetragonophthalma* and *Maypacius* are restricted to Africa, the monotypic genus *Polyboea* to Asia, and the genus *Perenethis* is widely distributed in Africa, Asia, and Australia. The African-Asian distribution pattern observed in this group of taxa occurs in other pisaurid and non-pisaurid spider groups as well. The cladogram obtained through the phylogenetic analysis suggests hypotheses regarding the origin of this distribution pattern.

METHODS

Specimens were made available by the institutions and their curators listed in the Acknowledgments. The institutional acronyms were taken from Arnett et al. (1993). Specimens designated and published as allotypes by original authors are in fact paratypes, specimens designated as néallotypes in subsequent publications have no validity under ICZN regulations (ICZN 1985).

Phylogenetic analysis of the *Perenethis* genus group.—*Outgroup:* The African pisaurid genera *Charminus* and *Cispius*, themselves sister taxa, serve as out-groups in the cladistic analysis. The membranous, sac-like anterior section of the female copulatory duct as it occurs in *Charminus camerunensis* Thorell 1899 (Fig. 5) and in all genera of the ingroup is the synapomorphy for ingroup and outgroup. The sister-group relationship of *Charminus* and *Cispius* is in this data set supported by one synapomorphy, the procurved ridge (= carina) of the epigynum (Figs. 4, 6). *Characters:* Character scoring is presented in Table 4. The character matrix contains 35 characters (17 binary, 18 multistate) with 98 states: 17 characters with 45 states from male copulatory organs, 11 characters with 31 states from female copulatory organs, and 7 somatic characters with 22 states. An artificial amalgam taxon of the genus *Cispius*, combining the female characters from *Cispius variegatus* Simon 1898 (type species of the genus, male unknown) and the male characters of *Cispius thorelli* Blandin 1978 (female unknown) was used in the data matrix. This procedure became necessary due to the scarcity of males in identified museum collections. The copulatory organs of *Cispius maruanus* (Roewer 1955), the only species for which both sexes are known, are similar to *variegatus* and *thorelli* respectively (Blandin 1978a, figs. 8, 19; only a single male specimen, the paratype, of *maruanus* is known). *Tree generation:* Trees were generated with the software package Hennig86, version 1.5 (Farris 1988), using the "ie*" command (implicit enumeration, calculates all possible shortest trees). All multistate characters were treated unordered (non-additive, implemented with the "ccode-;" command). *Character optimization:* Characters were optimized on the trees using CLADOS, version 1.2 (Nixon 1992), which permits comparing ACCTRAN and DELTRAN optimization (implemented in "Un Equis" Mode, using the commands "o" [ACCTRAN] and "CTL o" [DELTRAN]. Figure 2 shows the ACCTRAN optimization of characters, and Table 5 notes the characters that differ under DELTRAN optimization. Characters were mapped on the cladogram shown in Fig. 2 using the HOM = 0 (default) settings: Only those character state changes are indicated as homoplastic (white rectangles) that designate more than one independent origin of that state within this data set. Non-homoplastic character state changes are indicated as black rectangles.

Usage of terms.—*Character:* The term refers to an actual structure (e.g., conductor). Identical terms used for particular structures in male and female copulatory organs imply homology. A particular structure may appear in several different conditions (= character states). Morphologically indistinguishable character states were given identical codes in the data matrix, without *a priori* regard for the distribution of that particular state within the 14 species. To facilitate precise comparison of positions of various elements in the male genital bulb, the terms "proximal" and "distal" were used as defined below. *Male palpal organs:* Differing from common usage, the terms "proximal" and "distal" on the tegulum of the male palp refer to the position of a particular part in relation to the trajectory of the sperm duct. In all Pisauridae studied so far, the reservoir of the sperm duct forms a single spiral within the tegulum (Sierwald 1990, fig. 2). Following the course of the sperm duct, starting at the fundus in the subtegulum, apophyses inserting on the tegulum near the fundus are considered proximally located. Apophyses inserting closer to the ejaculatory duct, i.e., the embolic base, are referred to as being distal. Often these topological data can only be assessed in the expanded bulb. The terms dorsal, ventral, basal, apical, retrolateral, and prolateral are used descriptively for positions within the unexpanded bulb in ventral view. Dorsal and ventral refer to the position of a particular part being within the depth of the unexpanded genital bulb. Ventrally located parts are mostly visible in the unexpanded bulb in ventral view (as figured here). *Female copulatory organ:* The term epigynum refers to the external parts, the term vulva to the internal parts of the female copulatory organ. Copulatory duct describes that part of the duct that connects the copulatory opening with the spermatheca. Fertilization duct defines that part of the duct that connects the base of the spermatheca with the uterus externus. The spermatheca in Pisauridae consists of a rounded head, bearing pores, attached to the stalk of the spermatheca. The stalk of the spermatheca, containing the spermathecal duct, connects to the base of the spermatheca (Fig. 1b).

Dissections, measurements, drawings.—Dissections and drawings follow the procedure described in Sierwald 1989b, 1990. All measurements for body length, prosoma length and width and leg length are in mm. Recorded leg length in species descriptions is given for leg I. Leg segments were measured dorsally. Relative spine length is compared between taxa. The tibial spines are rather uniform in length on all legs of an individual and similar in length to most metatarsal and femoral spines (spines notated as "1" in Table 6), except when noted otherwise (spines notated as "i" or "I" in Table 6). To assess relative spine length a ratio was calculated by dividing the absolute length of one spine of the second pair of ventral spines of tibia I by the width of tibia I. The calculation was repeated for up to five individuals if available. A ratio of three indicates the spine being 3× as long as the

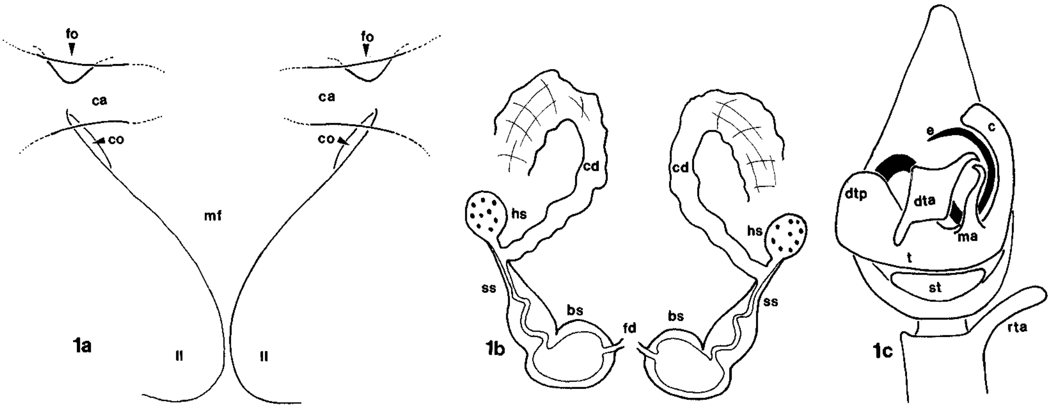


Figure 1.—Pisaurine copulatory organs, schematic. 1a, Female epigynum; 1b, Female vulva. 1c, Male palp.

tibia is thick. Eye arrangements were recorded in frontal view. The lens was measured in side view, perpendicular to the optical axis. Smaller specimens generally have relatively larger eyes than larger specimens of the same species. Eye size ratios may be reversed in extremely small or large specimens. Table 1 lists the abbreviations of terms.

PHYLOGENY AND ZOOGEOGRAPHY

The Pisaurinae Simon 1898.—Nineteen nominal genera listed in Table 2, including the genus *Pisaura* Simon 1885, form a clearly demarcated monophyletic group. All of these genera were originally placed in Simon's Pisaureae (Simon 1898), except the more recently described genera *Thalassiopsis* Roewer 1955, *Euprosthenopsis* Blandin 1974 and *Vuattouxia* Blandin 1979 (Table 2). For this clade, Simon's subfamilial name Pisaurinae is available. Table 3 lists genera previously assigned to the Pisaurinae, which are now removed from the here newly defined Pisaurinae. The affinities of the genus *Walrencea* Blandin 1979 are currently unknown (no specimens examined). The non-pisaurine genera listed in Table 3 and the remaining pisaurid genera formerly listed in the Thalassiinae and Thaumasiinae (Roewer 1954) cannot yet be grouped into monophyletic clades. Griswold (1993) noted in his analysis of lycosoid relationships that *Dolomedes* differs from *Pisaura* largely through the retention of plesiomorphic characters. Synapomorphies presently known for the Pisaurinae are: 1) The presence of a distal tegular apophysis in the male genital bulb (Fig. 1c) in addition to the median apophysis and the conductor, and 2) the presence of a ridge (= carina) with a pair of pits (= fossae) in the female epigynum. All members of the Pisaurinae for which the vulval structure is known have relatively small spermatheca, positioned at the posterior end of the vulva, with the copulatory duct communicating with the stalk of the spermatheca (Figs. 1a, 1b; for comparison with other pisaurid genera see Sierwald 1989b).

Characters of the Pisaurinae: Eye pattern: Eyes form two rows, PER recurved and wider than AER; PLE on low tubercles, PME equal or slightly smaller than PLE. AER recurved, straight or procurved. Several distinct character states of strongly procurved AER can be distinguished, i.e., character 2 states 2–4. ALE may be on tubercles in procurved AER. Eye sizes and ratios vary depending on size of specimens (see Methods). Chelicerae: Anterior margin always with three teeth, the middle tooth twice as large as the equally-sized lateral teeth. Posterior margin with 2, 3, or 4 teeth (Table 2), often genus specific. Spine pattern (Table 6): Spination of legs rather homogeneous within the subfamily, limited genus specific variations affecting few spines occur. Color pattern: Basic coloration of cuticle yellowish-brown to dark brown; gray to nearly black diffuse coloration located in the tissue directly beneath the integument (sternum, legs); white guanine in the opisthosoma, dorsally and ventrally. Patterns produced by colored hairs, dorsally two yellowish-to-white

Table 1.—Abbreviations on figures and in text.

Copulatory organs	
A	sclerite *A* at base of embolic division (♂)
bh	basal hematodocha (♂)
bmt	basal membranous tube (embolic division, ♂)
bs	base of spermatheca (♀)
c	conductor (♂)
ca	carina of epigynum (♀)
cd	copulatory duct (♀)
co	copulatory opening (♀)
db	dorsal branch of *dta* (♂)
ds	spermathecal duct (♀)
dst	distal sclerotized tube (embolic division, ♂)
dta	distal tegular apophysis (♂)
dtp	distal tegular projection (♂)
e	embolus (♂)
epf	epigynal folds (♀)
fd	fertilization duct (♀)
fo	fossae, epigynal pits on carina (♀)
hs	head of spermatheca (♀)
ll	lateral lobes of epigynum (♀)
lf	lateral flap at conductor
ma	median apophysis (♂)
mf	middle field between *ll* (♀)
p	petiolus (♂)
pp	pars pendula of embolus (♂)
rta	retrolateral tibial apophysis (♂)
ss	stalk of the spermatheca (♀)
st	subtegulum (♂)
t	tegulum (♂)
tr	truncus of embolus (♂)
vb	ventral branch of *dtp* (♂)
vta	ventral tibial apophysis (♂)
Legs	
Fe	femur
Pa	patella
Ti	tibia
Me	metatarsus
MeTa	metatarsus-tarsus
PaTi	patella-tibia
Eyes	
AE	anterior eyes
AER	anterior eye row
ALE	anterior lateral eyes
AME	anterior median eyes
PE	posterior eyes
PER	posterior eye row
PLE	posterior lateral eyes
PME	posterior median eyes
Miscellaneous	
ch	character, see Table 4

longitudinal stripes, rows of dark brown-to-black hairs often contrasting with the bright stripes. These color pattern elements occur also outside the Pisaurinae within the Pisauridae *sensu lato*, e.g., in *Dolomedes*. Leg spination (Table 6): Spination pattern uniform on certain leg segments throughout the Pisauridae *sensu lato* (e.g., Fe II, III), others show several, often genus-typical character states (e.g., patellar spination; see below in description of genera). Spine-length ratio: Small, thin-legged, web-living Pisauridae (e.g., *Polyboea*) with longer spines than medium-sized species hunting in vegetation (e.g., *Charminus*, *Pisaura*); short spines predominantly in large-sized species (e.g., *Maypacius* and *Tetragonophthalma*) (see Methods for calculation of ratio).

Female copulatory organ: (Figs. 1a,b). As in other Lycosoidea, the female copulatory organ consists of two lateral longitudinal folds, the epigynal folds (Sierwald 1989b). The internal pouches of these folds each contribute a copulatory duct, a spermatheca and a fertilization duct to the vulva. In the Pisaurinae, the epigynal folds run longitudinally, diverging (e.g., *Perenethis*) or converging anteriorly (e.g., *Charminus*) or forming curves (e.g., *Pisaura*). The copulatory opening is situated along the anterior section of the folds, thus the trajectory of the anterior section of the epigynal folds determines the position of the copulatory openings relative to other features within the female organs and the course of the anterior part of the copulatory duct in the vulva, e.g., whether it starts medially or laterally. In the genera *Afropisaura*, *Tetragonophthalma*, *Perenethis*, *Maypacius*, and to a lesser degree, *Polyboea*, the epigynal folds diverge strongly anteriorly, thus placing the copulatory openings laterally. Epigynum: The integument between (middle field, *mf*) and around the folds (lateral lobes, *ll*) is often strongly sclerotized and may form projections, grooves, pits, hoods, ridges, etc. When comparing the genera *Pisaura* and *Afropisaura*, Blandin (1976b) suggested interesting homology-hypotheses concerning the transverse ridge and the two pits (Fig. 1a). These elements can be identified in the epigyna of all 18 pisaurine genera. The integument anterior to the epigynal folds forms a transverse ridge (carina, *ca*) that can be straight, procurved or recurved, forming a large sclerotized lip, can be entire or separated in two branches. The

Table 2.—Variable characters in the Pisaurinae. [1] Originally described by Simon (1898a: 295) as *Caripeta* (name preoccupied), *Caripetella* nom. nov. by Strand (1928). [2] Data from Blandin 1979a. [3] Considered a synonym of *Nilus* by Simon (1889a: 296). ♂ males only known, ♀ females only known. Character states in parentheses ( ) refer to a variation occurring in few individuals within a species. Character states in brackets [ ] refer to a variation in a single species of the genus. Strongly procurved anterior eyes occur in distinctly different states (states: procurved I through IV) in the pisaurine genera.

					Cheliceral teeth	
	PME-Size	*ALE*-Size		*AER*-Shape	Number	Size
Afropisaura Blandin 1976	*PME>AME*	*ALE≥AME*	*ALE<PME*	proc/straight	3	equal
♀ *Caripetella* Strand 1928[1]	*PME>AME*	*ALE>AME*	ALE<*PME*	procurved	4	equal
Charminus Thorell 1899	*PME>AME*	*ALE=AME*	*ALE<PME*	recurved	3 (4)	unequal [equal]
Chiasmopes Pavesi 1883	*PME>AME*	*ALE>AME*	*ALE<PME*	procurved III	3	equal
Cispius Simon 1898	*PME>AME*	*ALE<AME*	*ALE<PME*	recurved (straight)	3 [2]	unequal
♀ *Cladycnis* Simon 1898[2]	*PME>AME*	*ALE<AME*	*ALE<PME*	recurved	3	unequal
Dendrolycosa Doleschall 1859	*PME>AME*	*ALE>AME*	*ALE>PME*	recurved	3	unequal
Euprosthenops Pocock 1897	*PME>AME*	*ALE>AME*	*ALE=PME*	procurved IV	3 (4)	equal
Euprosthenopsis Blandin 1974	*PME>AME*	*ALE>AME*	*ALE=PME*	procurved IV	3	equal
Maypacius Simon 1898	*PME<AME*	*ALE<AME*	*ALE=PME*	procurved II	2	equal
♀ *Paracladycnis* Blandin 1976	*PME>AME*	*ALE>AME*	*ALE<PME*	recurved	3	equal
Perenethis L. Koch 1878	*PME>AME*	*ALE<AME*	*ALE<PME*	procurved	2	unequal
Pisaura Simon 1885	*PME>AME*	*ALE>AME*	*ALE<PME*	straight	3	unequal
Polyboea Thorell 1895	*PME>AME*	*ALE>AME*	*ALE>PME*	procurved	2	equal
Rothus Simon 1898	*PME>AME*	*ALE>AME*	*ALE<PME*	procurved	3	equal
♀ *Tallonia* Simon 1889[3]	*PME=AME*	*ALE=AME*	*ALE=PME*	recurved	3	equal
Tetragonophthalma Karsch 1878	*PME>AME*	*ALE>AME*	*ALE=PME*	procurved I	4	equal
♂ *Thalassiopsis* Roewer 1955	*PME>AME*	*ALE>AME*	*ALE=PME*	recurved	3	equal
Vuattouxia Blandin 1979	*PME>AME*	*ALE>AME*	*ALE=PME*	procurved	3	equal

Table 3.—Systematic position of genera listed previously in the Pisaurinae by Simon (1898:282–297) and Roewer (1954:110–126). [1] Type species congeneric with *Dolomedes* based on description in Roewer (1955:190, figs. 73a, b). Also discussed by Blandin (1978:38). [2] Listed in Simon's Supplément Générale (1898:1045) and assigned to the Dolomedeae. [3] Specimens examined for this study. [4] Listed in the Supplément Générale (1898:1044) and assigned to Pisaureae.

Simon 1898	Roewer 1954	Current systematic position
Architis Simon 1898	*Architis*	Pisauridae sensu lato
	Cispiolus Roewer 1955	synonym of *Dolomedes*[1]
	Cispiomma Roewer 1955	synonym of *Cispius* (by Blandin 1978a:44)
	Enna Cambridge 1897[2]	transferred to Trechaleidae (by Carico 1986)
	Euprosthenomma Roewer 1955	synonym of *Euprosthenops* (by Blandin 1976:67)
Eurychoera Thorell 1897	*Eurychoera*	Pisauridae sensu lato[3]
Ischalea L. Koch 1872	*Ischalea*	transferred to Stiphidiidae
	Melocosa Gertsch 1937	transferred to Lycosidae
	Pelopatis Bishop 1924	Synonym of *Pisaurina* (by Carico 1972:297)
Phalaea Simon 1898	synonym of *Tetragonophthalma*	
Pisaurina Simon 1898	*Pisaurina*	Pisauridae sensu lato
Sisenna Simon 1898	*Sisenna*	transferred to Trechaleidae (by Sierwald 1990:51)
Spencerella Pocock 1898[4]	*Spencerella*	synonym of *Chiasmopes* (by Blandin 1974a:311)
Staberius Simon 1898	*Staberius*	Pisauridae sensu lato
Thanatidius Simon 1898	*Thanatidius*	synonym of *Pisaurina* (by Carico 1972:297)
Genera of currently unknown affinities		
	Cispinilus Roewer 1955	no specimens examined
Nilus O.P.—Cambridge 1876	*Nilus*	no specimens examined
	Phalaeops Roewer 1955	no specimens examined
Stoliczka O.P.—Cambridge 1885	*Stoliczka*	no specimens examined

carina possesses two lateral pits here termed fossae (*fo*). The fossae may be located directly above the copulatory openings, lateral to them or between them. Their positional relationship to the copulatory opening and additional depressions (e.g., as in *Afropisaura*) probably determine the fixation mechanism needed to securely connect the expanded male bulb and the epigynum. Thus, the Pisaurinae invite the study of copulation mechanics and its evolutionary change. Vulva: The slitlike copulatory openings lead into the mostly membranous, saccate copulatory ducts, often forming loops. In the genera *Afropisaura*, *Tetragonophthalma*, *Perenethis*, and *Polyboea* the copulatory duct possesses two large saccate loops, with the first loop running from the lateral copulatory opening towards the middle of the vulva. The copulatory ducts (*cd*) enter the stalk (*ss*) of the laterally located spermatheca close to the perforated spermathecal heads (*hs*). The coiled spermathecal ducts (*ds*) enter the large base of the spermatheca (*bs*), which contains either an enlarged lumen or additional coils of the duct. The coiling pattern of the spermathecal duct is often species-specific. The fertilization duct (*fd*) is short and sclerotized, originating at the medial portion of the spermathecal base. Such tri-partite spermatheca, consisting of head, stalk and base, has been found in many genera of Lycosoidea (Järvi 1905; Sierwald 1989b, Griswold 1993) and other members of the RTA-Clade (which comprises all families in which males possess a retrolateral tibial apophysis; Coddington & Levi 1991).

Male copulatory organ: The male copulatory organ of *Pisaura* has been described and figured in detail elsewhere (Sierwald 1990). The most conspicuous feature is the presence of three apophyses, the conductor (*co*) on the retrolateral side, the median apophysis (*ma*) and distal tegular apophysis (*dta*) ventrally in the center of the unexpanded bulb (Fig. 1c). The distal tegular apophysis represents a conspicuous synapomorphy for the Pisaurinae. The distal tegular apophysis was labelled fulcrum by Blandin (1976b) but is not homologous with the "fulcrum" *sensu* Comstock (1910) in *Dolomedes* (Sierwald 1990). In contrast to other pisaurid genera, members of the Pisaurinae possess a simple retrolateral tibial apophysis (*rta*) with a single rounded or pointed tip. A petiolus is well developed. The tegulum is bowl-like, with the sperm duct following the outer margin of the bowl. The upper surface of the tegulum is partly sclerotized but membranous around the base of the median apophysis and around the ventral branch of the distal tegular apophysis, permitting both to tilt out of their position during inflation. The distal tegular projection (*dtp*) is broadened and sclerotized, some with one or two humps. The base of the distal sclerotized tube of the embolic division appears to be supported by the sclerotized humps of the distal tegular projection during expansion of the bulb (Fig. 11).

The conductor (*co*), an outgrowth of the retrolateral tegular wall, displays several genus-typical character states within the Pisaurinae. An often strongly-sclerotized outer retrolateral wall and a more or less membranous inner prolateral wall that is partly inflatable are the basic components. The inner wall may feature membranous folds, along which the embolus rests in the unexpanded bulb (Figs. 8, 10). The conductor is a very important feature for the analysis of the Pisaurinae, since various parts of the conductor display several states (see under Character description below). The slender median apophysis (*ma*) is shorter than the distal tegular apophysis, with a sclerotized pointed tip often forming a hook. Its basal and prolateral sections are membranous and expandable. The large distal tegular apophysis (*dta*) has a dorsal (*db*) and a ventral branch (*vb*). The ventral branch anchors the distal apophysis in the tegulum, the dorsal branch connects to the basal membranous tube (*bmt*) of the embolic division. The shape of the ventral branch resembles a scapula and may carry a wing-shaped flap apically (Figs. 54, 57, 64). The ventral and dorsal branches are joined apically, forming a hook-shaped beak pointing retrolaterally. Next to the dorsal branch, within the basal membranous tube of the embolic division lies a sclerite labelled "*A*" in Figs. 11, 14, 29, 94, 96, 99. The sclerite is present in *Pisaura* (see Sierwald 1990, fig. 45, not labelled). In most species sclerite *A* is visible only in expanded palps. The embolic division, connected to the distal tegular projection via a membranous tube (basal membranous tube, *bmt*), consists of the distal sclerotized tube (*dst*), fused to the truncus of the embolus, and the pars pendula (*pp*). The embolus is of varying length and often whiplike.

Natural history.—Data on behavior and life history are scarce. Apparently, the majority of pisaurine spiders hunt in the vegetation. Members of a few genera, *Euprosthenops* Pocock 1897 (see Gerhardt & Kästner 1938) and *Polyboea* (see Koh 1989) build webs for prey capture. Very young *Pisaura mirabilis* hunt in webs (Lenler-Eriksen 1969); their webs resemble those built by young *Dolomedes* and young *Pisaurina* Simon 1898, and the permanent webs built by *Architis* (see Carico 1985; Nentwig 1985; Sierwald 1990). The copulatory behavior of *Pisaura mirabilis* is well known: The male presents a wrapped prey item to the female (Hasselt 1884; Bristowe 1958; Nitzsche 1988). Unfortunately, the copulatory behavior of other pisaurine species is unknown. Nursery-webs have been reported from *Pisaura mirabilis*, *Afropisaura* and other pisaurid genera outside the Pisaurinae (Sierwald 1990).

Specimens examined.—Members of the genera *Afropisaura*, *Charminus*, *Cispius*, *Maypacius*, *Perenethis*, *Polyboea*, and *Tetragonophthalma* examined for this study are listed below under the description of each genus. Other material: *Caripetella madagascariensis* (Lenz 1886): **MADAGASCAR**: *Fianarantsoa Province*, P.N. Ranomafana, Talatakely, 21°15′S, 47°25′E, 900 m, 1♀, 5–7 October 1993 (Scharff, Larcher, Griswold, Andriamasimanana) (currently CASC). *Toamasina Province*, P.N. Perinet, 1000 m, near Andasibe, 18°56′S, 48°24′E, 2♀, 4–5 November 1993 (Coddington, Larcher, Griswold, Andriamasimanana, Scharff) (currently CASC). *Antsiranana Province*, Marojejy Reserve, 8.4 km NNW Manantenina, 14°25′S, 49°45′E, 700 m, numerous ♂♀, 10–16 November 1993 (currently CASC). *Chiasmopes namaquensis* (Roewer 1955): **SOUTH AFRICA**: *Cape Province*, Die-Vlug, near Avontuur, fynbos dung trap, 1♀, 16–19 December 1981 (S. & J. Peck) (AMNH). *Chias-*

mopes sp.: **SOUTH AFRICA**: *Natal*, Cathedral Peak Forest, 75 km WSW of Estcourt, grassland, pan trap, 2♂, 13–31 December 1979 (S. & J. Peck) (AMNH). *C. hystrix* (Berland 1922): **SOUTH AFRICA**: *Transvaal*, Ohrigstad, 14 km S Belfast, 1♀, 27–29 December 1990 (V.D. & B. Roth) (CASC). *Dendrolycosa* sp.: **PHILIPPINES**: *Luzon*, Ilocos Norte, Pagudpud, Subec, 1♂, 23 May 1987 (C.K. Starr) (USNM). **MALAYSIA**: *Perak*, Cameron Highlands, 1♀ (Koh 84.06.12.10). *Pahang*, Fraser's Hill, 1♀ (Koh 76.11.16.08). **BRUNEI**: 1♀ with egg sac, (Koh 83.01.26.02). **PAPUA NEW GUINEA**: *Madang Province*, Nobonob Hill, 7 km NW Madang, 5°10′S, 145°5′E, 2♂, 1 May 1988 (W.J. Pulaski) (CASC). *Euprosthenops australis* Simon 1898: **TANZANIA**: Inside W. slope Ngorongoro Crater, 1850 m, 1♀, 21 October 1957 (E.S. Ross & R.E. Leech) (CASC). *Seronera*, Serengeti National Park, 1450 m, 1♀, 24 November 1967 (E.S. Ross & A.R. Stephen) (CASC). *Euprosthenops bayaonianus* (Capello 1866): **ZIMBABWE**: *Kariba*, 2♂, 16 August 1990 (V.D. & B. Roth) (CASC). **ZAIRE**: *Faradje III*. Lessert det., 1♀ (AMNH). *Euprosthenops biguttatus* Roewer 1955: **ZIMBABWE**: *Mazabuka*, Matthysse leg., 1♂, 17 September 1952 (AMNH). **ANGOLA**: *Lunda Province*, Nova Chavez, 1♀, 14–16 September 1949 (B. Malkin) (CASC). *Euprosthenopsis* sp.: **SOUTH AFRICA**: *Transvaal*, Klaserie, Guernsey Farm, 1♂, 18–31 December 1985 (S. & J. Peck) (AMNH). *Cape Province*: Table Mountain, Skeleton Gorge, 34°S, 18°30′E, 1♀, 13 February 1991 (V.D. & B. Roth) (CASC). **KENYA**: *Rift Valley Province*, Lake Naivasha, Fisherman's Camp, *ca.* 0°45′S, 36°20′E, 1♂, 19 October 1992 (V.D. & B. Roth) (CASC). **KENYA**: 49 mi NW of Mobasa, 450 m, 1♀, 4 November 1957 (E.S. Ross & R.E. Leech) (CASC). **TANZANIA**: NE side of Mt. Meru, 1500 m, 1♀, 28 October 1957 (E.S. Ross & R.E. Leech) CASC). *Euprosthenopsis armatus* (Strand 1913): **ZAIRE**: *Garamba*, 1♂ (AMNH). **ZIMBABWE**: *Harare*, 3♀, 14 August 1990 (V.D. & B. Roth) (CASC). *Eurychoera quadrimaculatus* Thorell 1897: **SINGAPORE**: MacRitchie Reservoir, 1♀ (Koh 77.01.01.01), 1♂ (Koh 88.020.06). *Paracladycnis vis* Blandin 1979: **MADAGASCAR**: *Antananarivo*, 1♀, several juv., 13 February 1952 (V.J. Tipton) (AMNH); 2♀, 19 February 1992 (V. Roth) (CASC). *Mandraka*, 18°56′S, 47°56′E, 1♀, 10 March 1994 (W.J. Pulawski) (CASC). *Ranomafana*, I. Fanadiana town, 1♀, 16 May 1992 (Roth) (CASC). *Pisaura mirabilis* (Clerck 1757): **GERMANY**: *Bayern*, Spessart, Neuhütten, Zilch leg., 1♀, 19 June 1949 (AMNH ex SMFD). *Ransonia mahasoana* Blandin 1979: **MADAGASCAR**: *Fianarantsoa Province*, P.N. Ranomafana, Vohipara, 21°14′S, 47°24′E, 900 m, 2♀, 5–7 December 1993 (Scharff, Larcher, Griswold, Andriamasimanana) (currently CASC). *Antananarivo Province*, Ambohimanga, 18°44′S, 47°34′E, 1400 m, 2♂11♀, 1 November 1993 (Coddington, Larcher, Griswold, Andriamasimanana, Scharff) (currently CASC). *Antsiranana Province*, Marojejy Reserve, 8.4 km NNW Manantenina, 14°25′S, 49°45′E, 700 m, several ♂♀, 10–16 November 1993 (currently CASC). *Rothus purpurissatus* Simon 1898: **KENYA**: *Lake Nakuru*, N.P. campsite in Yellow Fever Forest, 1♀, 14 May 1975 (Penniman) (AMNH). **SOUTH AFRICA**: *Natal*, Lake Midmar, 1♂3♀, 6 January 1991 (V.D. & B. Roth) (CASC). *Tallonia picta* Simon 1889: **MADAGASCAR**: *Province Antsiranana*: Nosy Be, Lokobe Forest, 13°24′58.8″S, 48°18′26.5″E, 4♀, 11–14 August 1992 (V.D. & B. Roth) (CASC). Montagne d'Ambre, 12°30′57″S, 49°11′04″E, 2♀, 12 August 1992 (V.D. & B. Roth) (CASC). *Thalassiopsis vachoni* Roewer 1955: **MADAGASCAR**: *Maroantsetra*, 1♂, SMFD RII/10552/102 (type-label carries an invalid manuscript name). *Vuattouxia* Blandin 1979 sp.: **MADAGASCAR**: *Toamasina Province*, P.N. Perinet, near Andasibe, 1000 m, 18°56′S, 48°24′E, 4♂5♀, 4–5 November 1993 (Coddington, Larcher, Griswold, Andriamasimanana, Scharff) (currently CASC); 18°55′S, 48°25′E, 1♂1♀, 1–3 August 1992 (V.D. & B. Roth) (CASC). *Chutes de la Mort*, 1♂, 10 November 1959 (E.S. Ross) (CASC). *Fianarantsoa Province*, P.N. Ranomafana, Talatakely, 21°15′S, 47°25′E, 900 m, 5♀, 5–7 December 1993 (Scharff, Larcher, Griswold, Andriamasimanana) (currently CASC).

Phylogenetics.—The pisaurine genera *Charminus*, *Cispius*, *Tetragonophthalma*, *Afropisaura*, *Perenethis*, *Maypacius*, and *Polyboea* form the monophyletic *Perenethis* genus group, within the Pisaurinae as here defined. The synapomorphy for this genus group is the membranous saclike copulatory duct forming two large loops at least in some species of each of the seven genera except in *Cispius*. The genera *Charminus* and *Cispius*, themselves sister taxa, were designated as outgroup during the cladistic analysis (see above under METHODS). The sistergroup relationship between *Cispius* and *Charminus* is supported by the procurved carina, which is unique within the Pisaurinae. The outgroup genera were not newly revised for the present study and the character states of the type species of each genus were used in the cladistic analysis. However, most character states (Table 4) are identical in all known species of each genus as illustrated in Blandin's (1978a) revision of the genera. Characters of the internal female copulatory organ (*cha* 13–17) and a few character states in the male organs (*ch* 31, 33, 34), not illustrated by Blandin, were assessed in two species in *Charminus* (*C. camerunensis* and *C. aethiopicus*). In *Cispius*, the male characters were assessed in three different species (*C. thorelli*, *C. problematicus* and *C. bidentatus*), the female characters are based on the type species alone (*C. variegatus*).

Character description: Somatic characters. Character 0: Number of cheliceral teeth; 0 = three teeth, 1 = four teeth (with occasional occurrence of three teeth at one of the chelicerae), 2 = two teeth. Three cheliceral teeth is the most common and widely distributed character state in the Pisaurinae and thus assumed to be the primitive condition (see Table 2). However, the character is somewhat homoplastic within the Pisaurinae, e.g., the state two teeth occurs in *Cispius bidentatus* (Lessert 1936), all other species of the genera *Charminus* and *Cispius* have three cheliceral teeth. Character 1: Size of cheliceral teeth; 0 = unequal, 1 = equal. The character displays homoplasy within this data set and outside (e.g., *Charminus ambiguus* (Lessert 1925) has three equally-sized teeth). Character 2: Shape of AER; 0 = recurved, 1 = straight, 2 = procurved, 3 = strongly procurved [= st proc I in Table 2], 4 = extremely procurved [= st proc II in Table 2]. The morphological difference in the AER in *Maypacius* and *Tetragonophthalma* justifies a separate coding (see Blandin's figures, 1974a, figs. 1, 4). Character 3: Size ratio of ALE to PME; 0 = ALE<PME, 1 = ALE=PME, 2 = ALE>PME. Character 4: Size ratio of ALE to AME; 0 = ALE<AME, 1 = ALE=AME, 2 = ALE>AME. Character 5: Patella spination; 0 = patella with one dorsal apical spine as in *Charminus* (Table 6), 1 = patella with two dorsal and two lateral spines as in *Afropisaura*, 2 = patella of legs I and II without spines, patella II and IV with a single dorsal apical spine, as in *Tetragonophthalma*. Character 6: Spine length, expressed as ratio of length of tibial spine of second ventral spine-pair to width of tibia; 0 = 3, 1 = 1–1.5, 2 = 6.5. Extremely long (state 2) or short spines (state 1) are not as common in Pisauridae as moderate spine length (state 0).

Female copulatory organ: Character 7: Trajectory of epigynal folds; 0 = anterior section of epigynal folds convergent and close together (Figs. 4, 6), 1 = anterior section of epigynal folds divergent and far apart (e.g., Figs. 17, 20). Character 8: Carina; 0 = continuous (Figs. 4, 6, 17, 20, 23, 85, 88), 1 = separated into two distinct lateral, nearly straight branches (e.g., Fig. 31). Character 9: Carina form; 0 = recurved (Figs. 17, 20, 23, 82), 1 = straight (e.g., Figs. 31, 88), 2 = procurved as in the outgroup (Figs, 4, 6), 3 = undulated as in *Tetragonophthalma* (Fig. 23), 4 = undulated as in *Perenethis* symmetrica (Fig. 34). A recurved carina (state 0) occurs in many pisaurine spiders. Character 10: Posterior edge of carina; 0 = ridgelike (e.g., Fig. 31), 1 = liplike, overhanging anterior section of epigynal folds (e.g., Figs. 17, 23, 88). Character 11: Anterior edge of carina; 0 = weakly developed (Figs. 4, 6), 1 = distinctly developed, ridgelike (e.g., Figs. 17, 20, 31, 82, 85, 88). Character 12: Position of fossae in relation to copulatory opening; 0 = directly above copulatory openings (Figs. 17, 20, 23), 1 = above and lateral to copulatory opening (e.g., Figs. 4, 6, 42, 45), 2 = above and between copulatory openings (Figs. 82, 85, 88). Fossae directly above the copulatory openings appear to prevail in the Pisaurinae, thus this state is coded as 0. Character 13: Copulatory duct; 0 = membranous (e.g., Figs. 532, 35, 89), 1 = posterior section sclerotized (Figs. 83, 84), 2 = anterior and posterior sections sclerotized with membranous middle section (Figs. 18, 21), 3 = fully sclerotized over its entire length (*Tetragonophthalma*, Fig. 23). Character 14: Number of loops of copulatory duct; 0 = single loop (Figs. 7, 83, 86), 1 = two loops (e.g., Figs. 5, 32, 35, 89), 2 = two and one half loops (Figs. 18, 21, 24). Character 15: Copulatory duct loop sizes; 0 = first loop larger than second loop (e.g., Figs. 5, 49, 89), 1 = first loop equal to second loop (Figs. 24, 35). Character 16: Position of head of spermatheca; 0 = pointing laterally (e.g., Figs. 5, 19), 1 = pointing anteriorly (e.g., Figs. 7, 22), 2 = bent (Fig. 33). In the bent position, the *hs* points anteriorly, but the stalk immediately behind it is bent, thus the spermathecal duct does not run straight in that section. Character 17: Spermathecal base; 0 = with large lumen (Figs. 7, 22, 38, 41, 44, 47, 50), 1 = with small lumen, does not fill base of spermatheca (Figs. 5, 33, 35, 90), 2 = base filled with loops of spermathecal duct (Figs. 19, 24). Displays homoplasy within the genera *Afropisaura*, *Perenethis*, and *Maypacius*.

Male copulatory organ: Characters for the male of *Maypacius kaestneri* were taken from

Table 4.—Character scoring. The character matrix does not contain autapomorphies of terminal taxa (e.g., flap at the conductor in *Charminus*), unless they are part of a multistate series. Non-applicable character states indicated by "–". Unknown character states indicated by "?".

	Ch. camerunensis	*Ci. variegatus*	*A. valida*	*A. ducis*	*T. vulpina*	*Pe. simoni*	*Pe. symmetrica*	*Pe. dentifasciata*	*Pe. sindica*	*Pe. venusta*	*Po. vulpina*	*M. roeweri*	*M. kaestneri*	*M. petrunkevitchi*
Somatic characters														
0) Cheliceral teeth #: 3; 4(3); 2	0	0	0	0	1	2	2	2	2	2	2	2	2	2
1) Chel. teeth size: unequal; equal	0	0	1	1	1	0	0	0	0	0	1	1	1	1
2) AER rec; str; proc; strongly proc; extremely proc	0	0	1	2	3	2	2	2	2	2	2	4	4	4
3) ALE<PME; ALE=PME; ALE>PME	0	0	0	0	1	0	0	0	0	0	2	1	1	1
4) ALE<AME; ALE=AME; ALE>AME	1	0	1	2	2	0	0	0	0	0	2	0	0	0
5) Patellar spines: 1; 4; 0 and 1	0	0	1	1	2	0	0	0	0	0	0	0	0	0
6) Spine length to tibia width: 3;1–1.5; 6.5	0	0	0	0	1	0	0	0	0	0	2	1	1	1
Female characters														
7) anterior *epf*: convergent; divergent	0	0	1	1	1	1	1	1	1	1	1	?	1	1
8) carina: continuous; two branches	0	0	0	0	0	1	1	1	1	1	0	?	0	0
9) carina: rec; str; proc; *Tetragonophthalma*; *P. symmetrica*	2	2	0	0	3	1	4	1	1	1	1	?	1	0
10) Posterior edge of *ca*: ridge; lip	0	1	1	1	0	0	0	0	0	1	?	0	0	0
11) anterior edge of *ca*: weak; strong	0	0	1	1	1	1	1	1	1	1	1	?	1	1
12) position of fossae: directly above copulatory openings; lateral; between	1	1	0	0	0	1	1	1	1	1	2	?	2	2
13) copulatory duct: membraneous; posterior section sclerotized; posterior and anterior section sclerotized; fully sclerotized	0	3	2	2	3	0	0	0	0	0	0	?	0	1
14) *cd* loops: 1; 2; 2½	1	0	2	2	2	1	1	1	1	1	1	?	0	0
15) *cd* loop sizes: 1 > 2; 1 = 2;	0	–	0	0	1	0	1	0	0	0	0	?	–	–
16) *hs* position: lateral; anterior; bent	0	1	0	1	1	2	2	0	2	2	2	?	2	1
17) *bs*: large lumen; small lumen; lumen filled with duct loops	1	0	2	0	2	1	1	0	0	0	1	?	0	1
Male characters														
18) *rta* shape: round-perpendicular; flat-forward	0	0	0	0	0	1	1	?	1	1	0	1	0	?
19) *rta* tip: pointed; rounded	0	0	0	0	1	1	1	?	0	0	0	0	?	?
20) tibial venter: smooth; with hump	0	0	0	0	0	1	1	?	1	1	0	0	0	?
21) tegulum base: smooth; with peak	0	0	0	0	0	1	1	?	1	1	1	1	1	?
22) *c* tip: long; short	0	0	1	1	0	0	0	?	0	0	0	0	0	?
23) *c* midpiece: long; short	0	0	0	0	0	0	0	?	0	0	0	1	1	?
24) *c* tip: broad round; slender round; spiral; modified spiral	0	0	–	–	0	1	1	?	1	1	2	3	3	?
25) *c* base: narrow; broad	0	0	1	1	1	0	0	?	0	0	0	0	0	?
26) *c* mesally: smooth; with hump	0	0	0	0	0	1	1	?	1	1	0	0	0	?
27) *c* tip: with ridge-like fold; smooth	0	0	1	1	0	1	1	?	1	1	0	0	0	?
28) *c* tip: additional guiding lamella absent/present	0	0	0	0	0	0	0	?	0	0	1	1	1	?
29) *db* of *da* smooth; with pit	0	0	0	0	0	0	0	?	0	0	1	1	?	?
30) scl *A* size: small; median; large	1	1	1	1	0	0	0	?	0	0	2	2	?	?
31) scl *A* shape: triangular; rod; small, oval; forked	0	0	3	1	1	2	2	?	2	2	3	3	?	?
32) *dst* shape: *Ch*; *Ci*; *Afro*; *Tetra*; *Pe*; *PoMay*	0	1	2	2	3	4	4	?	4	4	5	5	?	?
33) *e* length: long; moderate; short	0	1	0	0	0	0	0	?	0	0	1	2	2	?
34) *pp* length: short; ½ to ¾; total *e* length	0	2	1	1	1	1	2	?	1	1	0	1	?	?

Blandin's figure (1975a: 389, figs. 21, 22). Character 18: Retrolateral tibial apophysis (RTA); 0 = round and perpendicular to palpal tibial (e.g., Figs. 9, 12–15, 25, 27, 97), 1 = flat and parallel to cymbium (e.g., Figs. 54—59, 91). Character 19: Tip of RTA; 0 = pointed (e.g., Figs. 14, 59), 1 = rounded (Figs. 28, 56, 58). Character 20: Tibial venter; 0 = smooth (e.g., Figs. 11, 15, 92, 97), 1 = with hump-shaped apophysis (Figs. 54, 55, 58, 79). Character 21: Tegulum base; 0 = smoothly rounded (e.g., Figs. 8, 10, 25, 29), 1 = with basal protuberance at retrolateral side of unexpanded bulb (unique within the Pisaurinae, Figs. 54, 92, 97). Character 22: Conductor tip length; 0 = long (e.g., Figs. 10, 58), 1 = short (Fig. 25). Character 23: Conductor midpiece between tip and base; 0 = long (e.g., Figs. 13, 55, 57), 1 = short (Figs. 91, 95). Character 24: Conductor tip shape; 0 = broad and well rounded (Figs. 10, 12, 27) as in the outgroup, 1 = slender and rounded as in Perenethis (Figs. 54–58), 2 = modified, with a spiral tip as in *Polyboea* (Figs. 97, 98), 3 = modified as in *Maypacius* (Fig. 93). Character 25: Base of conductor; 0 = narrow (Figs. 55, 95, 98), 1 = broad (Figs. 26, 28). Character 26: Conductor mesal margin; 0 = smooth, 1 = with mesal inflatable hump as it occurs in *Perenethis* (Fig. 55). Character 27: Conductor tip folds; 0 = conductor tip with a ridgelike fold formed by the membranous inner conductor wall as in *Charminus* and *Tetragonophthalma* (Fig. 10, 12, 27), 1 = inside of tip smooth (Fig. 56). Character 28: Posterior guiding lamella at tip of conductor; 0 = absent (Fig. 10), 1 = present (Figs. 95, 98). Character 29: Dorsal branch of distal tegular apophysis; 0 = smooth, 1 = with pit (Figs. 95, 98). The morphological similarity in the distal tegular apophysis between *Polyboea* and *Maypacius* is striking and links both genera. Character 30: Size of sclerite *A*; 0 = small (Fig. 29), 1 = medium (Figs. 11, 14, 15), 2 = large (Figs. 94, 99). This sclerite can only be seen in the expanded bulb. As far as known, a small sclerite *A* is widely distributed within the Pisaurinae. Character 31: Sclerite *A* shape; 0 = triangular, as in Charminus and *Cispius* (Figs. 11, 14), 1 = rod-shaped, as in *Tetragonophthalma* (Fig. 29), 2 = small, elongated oval, as in *Perenethis*, 3 = large, one end forked as in *Afropisaura valida*, *Polyboea* and *Maypacius* (Figs. 91, 93, 99). Character 32: Shape of sclerotized tube of embolic division; 0 = as in *Charminus*, 1 = as in *Cispius*, 2 = as in *Afropisaura*, 3 = as in *Tetragonophthalma*, 4 = as in *Perenethis*, 5 = as in *Polyboea* and *Maypacius*. Character 33: Embolus length; 0 = long (Figs. 11, 25, 26, 28, 54, 57), 1 = moderate (Fig. 14, 99), 2 = short (Fig. 95). Character 34: Length of pars pendula alongside the embolus; 0 = short (Figs. 11, 99), 1 = ½–¾ along the embolus (Figs. 26, 28, 56), 2 = total embolus length to its tip (Figs. 14, 15, 58).

Analysis: Hennig86 runs containing all characters (multistate characters unordered) resulted in three equally parsimonious, highly resolved trees of 87 steps, with a consistency index (*ci*) of 0.72 and a retention index (*ri*) of 0.76, differing only in the resolution of the three species of the genus *Maypacius*. The equally long Nelson Consensus Tree (Fig. 2), is part of the original series of three trees, and places these three species in an unresolved trichotomy. An inspection of the other two, mutually exclusive trees presenting the three species fully resolved, showed that the resolution is based on presumed character states of missing characters. Only in two of the nine species of the genus *Maypacius* are the males and females known, and few specimens are available for study (see below under *Maypacius*), causing this lack of data. Optimization of character-state changes may differ with the choice of optimization schemes, ACCTRAN (depicted here in Fig. 2) or DELTRAN. In the following description, only non-homoplastic character-state changes supporting a clade under both optimization schemes are discussed, unless noted otherwise.

The Ingroup (clade A), containing the genera *Tetragonophthalma*, *Afropisaura*, *Perenethis*, *Maypacius*, and *Polyboea* is defined by the following synapomorphies of non-homoplastic character-state changes: Procurved anterior eye row (*ch* 2), the shape of epigynal folds (*ch* 7), the strongly developed anterior edge of the carina (*ch* 11), and a pars pendula ½–¾ along the embolus (*ch* 34). The genera *Afropisaura* and *Tetragonophthalma* (clade B) form the sister-group to clade C. The sister-group relationship between *Afropisaura* and *Tetragonophthalma* is supported by five non-homoplastic character-state changes: The position of the fossae above the copulatory openings (*ch* 12), the undulated posterior sec-

Table 5.—Character performance. *Different optimizations ACCTRAN/DELTRAN.

Character number	Character states	Steps	ci	ri
0)	m (3)	2	100	100
1)	b	2	50	83*
2)	m (5)	4	100	100
3)	m (3)	3	66	66*
4)	m (3)	4	50	33
5)	m (3)	2	100	100*
6)	m (3)	3	66	66*
7)	b	1	100	100
8)	b	1	100	100
9)	m (5)	5	80	66*
10)	b	2	50	66
11)	b	1	100	100
12)	m (3)	2	100	100
13)	m (4)	4	75	50*
14)	m (3)	3	66	75
15)	b	2	50	0
16)	m (3)	5	40	40
17)	m (3)	5	40	40
18)	b	2	50	75
19)	b	2	50	50
20)	b	1	100	100
21)	b	1	100	100
22)	b	1	100	100
23)	b	1	100	100
24)	m (4)	3	100	100*
25)	b	1	100	100
26)	b	1	100	100
27)	b	2	50	80
28)	b	1	100	100
29)	b	1	100	100
30)	m (3)	3	66	75*
31)	m (4)	4	75	75*
32)	m (6)	5	100	100*
33)	m (3)	3	66	50*
34)	m (3)	4	50	0*

tion of the copulatory duct (*ch* 14), copulatory duct with 2½ loops), spermathecal base filled with loops of spermathecal duct (*ch* 17, reversal in *Afropisaura* ducts), the broad base of the conductor (*ch* 25), and the rod-shaped sclerite A (*ch* 31). Non-homoplastic apomorphies for the genus *Afropisaura* are the spination of the patella (*ch* 5), the partly sclerotized copulatory duct (*ch* 13), the short pointed conductor (*ch* 22), and—under DELTRAN optimization—the peculiar shape of the distal sclerotized tube of the embolic division (*ch* 32). Clade C (sister taxon to clade B), containing the genera *Perenethis*, *Polyboea* and *Maypacius* is supported by the loss of one cheliceral tooth (*ch* 0), the straight carina (*ch* 9, with special form in *P. symmetrica* and recurved carina in *M. petrunkevitchi* Lessert 1933), the bent spermathecal head (*ch* 16, with reversals in *P. symmetrica* and *M. petrunkevitchi*), and the basal protuberance at the tegulum (*ch* 21). The sister-group relationship of *Polyboea* and *Maypacius* (clade D) is corroborated by mesal position of the fossae (*ch* 12), the additional guiding lamella in the conductor (*ch* 28), the pit in the dorsal branch of the distal tegular apophysis (*ch* 29), the large, forked sclerite *A* (*ch* 30), and—under ACCTRAN optimization—the shape of the distal sclerotized tube of the embolic division (*ch* 32). The species of *Maypacius* included in this study are defined by the strongly procurved anterior eye row (*ch* 2), the short conductor midpiece (*ch* 23), and—under ACCTRAN—the short embolus (*ch* 34).

The genus *Perenethis*, the sister taxon of clade D, is defined by four apomorphies of non-homoplastic character-state changes: Carina with two branches (*ch* 8), the ventral tibial apophysis (*ch* 20), the slender, rounded tip of the conductor (*ch* 24), the mesal hump at the conductor (*ch* 26), and—under DELTRAN—the shape of the distal sclerotized tube of the embolic division (*ch* 32). The sister-group relationship of the African species, *Perenethis simoni* and *Perenethis symmetrica*, is weakly supported by a homoplastic character-state change, the rounded tip of the retrolateral tibial apophysis (*ch* 19). The Asian-Australian species of the genus are weakly supported by the large lumen in the spermathecal base (*ch* 17), a very homoplastic character throughout the Pisaurinae. The cladogram clearly demonstrates that the astounding phenetic similarity between *P. simoni* (Lessert 1916), *P. sindica* (Simon 1897) and *P. venusta* L. Koch 1878 is based on symplesiomorphies alone and suggests, however weakly, that the African species and the Asian species of *Perenethis* form separate clades.

Zoogeography.—Pisaurine genera are predominantly African (south of the Sahara), but one genus, *Polyboea*, is restricted to southeast Asia. *Pisaura* itself occurs in Europe and Asia. The distribution patterns within the Pisaurinae display an interesting peculiarity: Three genera, *Perenethis*, *Dendrolycosa* (genus unrevised, Blandin 1979a, figs. 30, 34, 36)

Table 6.—Leg spination patterns of *Charminus,* typical for the Pisaurinae. Genus specific variations shown below. Abbreviations: 1 = average size spine; i = short spine; I = long spine; * = spine dislocated to retrolateral; v = spine dislocated to ventral; 2 = spine pair, average length; ii = spine pair, spines short. Notation indicates location of spine on leg segment, e.g., proximal, apical, and to other spines of segment. Spine length [ventral tibial spine, second pair, first leg]: spine length : tibia width = 3 set as normal length.

Charminus

leg		*Fe*	*Pa*	*Ti*	*Me*
leg I	do	1 1 1	1	1* 1	ii
	pl	i 0 0 I 1		1 1^{v}	1 1 1
	rl	1 1 1 1 1		1 1	1 1 1
	v			2 2 2 ii	2 2 i
leg II	d	1 1 1	1	1* 1	ii
	pl	1 1 1 1 1		1 1^{v}	1 1 1
	rl	1 1 1 1 1		1 1	1 1 1
	v			2 2 2 ii	2 2 i
leg III	do	1 1 1	I	1* 1	ii
	pl	1 1 1 1 1		1 1^{v}	1 1 1
	rl	1 1 1 1 1		1 1	1 1 1
	v			2 2 ii	2 2 i
leg IV	do	1 1 1	1	1* 1	ii
	pl	i i 1 1 1		1 1^{v}	1 1 1
	rl	0 0 0 1 1		1 1	1 1 1
	v			2 2 ii	2 2 i

Afropisaura

leg		*Fe*	I-IV *Pa*
leg I	do	1 1 1	i 1
	pl	0 1 1 I 1	i
	rl	1 1 1 1 1	i

Tetragonophthalma

leg		*Fe*	I, II *Pa*	III, IV *Pa*
leg I	do	1 1 i	0	1.
	pl	i 1 1 I 1		
	rl	1 1 1 1 1		

		I, II *Ti*	III, IV *Ti*
♀ leg I,II	do	0	1* 1
	pl	1 1^{v}	1 1
	rl	1 1	1 1
	v	2 2 2 ii	2 2 ii

		Ti	III, IV *Ti*
♂ leg	do	(1*) 1	1* 1
	pl	1 1^{v}	1 1^{v}
	rl	1 1	1 1
	v	2 2 2 ii	2 2 ii

Polyboea

leg		*Fe*	I-IV *Ti*
leg I	do	1 I i	1* 1
	pl	0 I^{v}I^{v}I^{v}1	1 1^{v}
	rl	1 1 1 1 1	1 1
	v		2 2 2 0

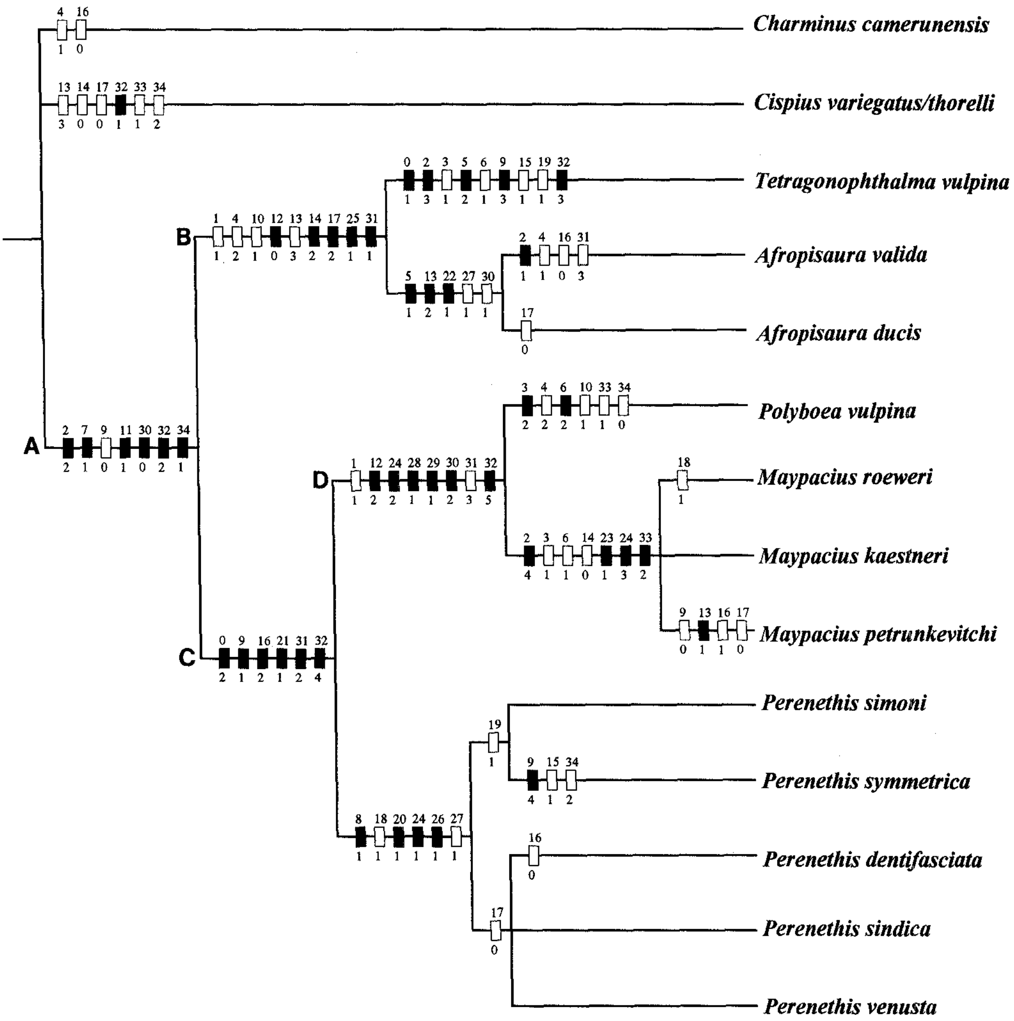


Figure 2.—Preferred Cladogram (identical to Nelson Consensus Tree). ACCTRAN character optimization; character mapping: black rectangles = non-homoplastic character state origination, white rectangles = homoplastic character state origination [implemented in CLADOS by setting homoplasy indicator, HOM=0].

and *Euprosthenops* (Blandin 1975b), contain both African and Asian species.

In the genus *Perenethis*, two species, *P. simoni* and *P. symmetrica*, occur in Africa (Fig. 3); three species, *P. sindica*, *P. dentifasciata* and *P. fascigera* are distributed in Asia (including India and Sri Lanka); and one species, *P. venusta* occurs in Australia and the Bismarck-Archipelago. *Maypacius*, the sister taxon of the Asian genus *Polyboea*, is restricted to Africa. This specific pattern, the distribution of closely related species in Africa south of the Sahara and Asia/Australia, can be found in other Pisauridae *sensu lato* as well. The pisaurid genus *Thalassius*, presumably a relative of the worldwide genus *Dolomedes*, shows a similar pattern. Eight species of the genus *Thalassius* occur in Africa, and four species in Madagascar. A single species, *T. jayacari* F.O. Pickard-Cambridge 1898, is found in the Middle East; and two species, *T. albocinctus* (Dolescall 1859) and *T. phipsoni* F.O. Pickard-Cambridge 1898, are distributed in south-east Asia, including China, the Philippines and Singapore (Sierwald 1987). There are other groups displaying an African-Southeast Asian distribution of close relatives, e.g., the tropical tree-frog subfamily Rhacophorinae (family Ranidae) (Savage 1973), the genus *Francolinus* among the galliform birds (Dinesen et al. 1994), several members of the bird family Rallidae (Olson 1973), and members of the plant family Sapotaceae (Pennington 1991).

Africa, South America and India (together with Madagascar) formed a contiguous land mass about 155 million years before present. Madagascar separated from Africa over 120 m.y.b.p. and South America separated from Africa about 95 m.y.b.p. (Smith et al. 1994). Since no member of the *Perenethis* genus group has been recorded from Madagascar or the Americas so far, it is unlikely that the origin of the terminal taxa studied here dates back more than 100 million years. When optimizing the current distribution of the terminal taxa like a character on the proposed cladogram (Fig. 3) it is most parsimonious to assume an African origin for the group. Using Bremer's (1992) method to reconstruct the ancestral area of the group under study here, yields the same result. Assuming an African distribution of early pisaurine taxa requires a hypothesis regarding the presence of *Polyboea* and *Perenethis* in Asia and Australia. Two independent events, one in clade D and another within *Perenethis*, have to be proposed to account for the current distribution pattern. According to Axelrod & Raven (1978), lowland rain forest and subtropic rain forest covered most of Africa during the Paleocene (60 m.y.b.p.), thus ancestors of the group under study were likely to be more widely distributed in Africa than today, where they are mostly restricted to Africa south of the Sahara. At that time, the Tethys Sea was an effective barrier between Africa and Asia. In the mid-Miocene (15 m.y.b.p.) a land bridge formed between Africa and Arabia, connecting the African land mass with Asia. During the Miocene, the exchange of mammalian taxa between Africa and Asia increased dramatically presumably via this land bridge, resulting in a significant decrease of mammalian taxa endemic to Africa in the Pliocene. A two-way traffic via the Arabian Peninsula affected the composition of both faunas in Asia and Africa (Magglio 1978). The habitat conditions along that passage-way were suitable at various times during the Cenozoic for many large mammals, indicating the existence of vegetation cover. Savage (1973) explains the African-Asian distribution of the tropical tree-frog subfamily Rhacophorinae (Family Ranidae) as an immigration from Africa to Asia during the early Cenozoic. Dinesen et al. (1994) also assume that the African-Asian distribution of several related forest birds can be explained by alternations of isolation and range expansion opportunities via an African-Arabian land bridge to Asia.

The blockage of the Tethys Sea by a land bridge between Africa (including Arabia) and Asia in the mid-Miocene (15 m.y.b.p.) with subsequent alteration of the latitudinal air-ocean circulation produced a drier climate in northern Africa (Crowell & Frakes 1970) and caused the expansion of savanna and sclerophyll vegetation over northern Africa and the Sahara region (Axelrod & Raven 1978). The hot, dry Saharan-Libyan desert did not develop before the Pleistocene. To my knowledge, no Pisauridae *sensu lato* have been reported from very arid habitats. Judging from their current habitat preferences, deserts and high mountainous areas may be the most difficult areas to cross, thus presenting effective barriers. The restriction of most pisaurine taxa to the south of the Sahara supports this notion. At least two independent events have to be assumed for the *Perenethis* genus group to account for the occurrence of species of this group in Asia. Instead of invoking hypotheses of chance dispersal (e.g., ballooning) over preexisting barriers like the Sahara, range expansions of the respective ancestral species by tracking the expansion of suitable habitats across the mid-Miocene (15 m.y.b.p.) land bridge between Africa (including Arabia) and Asia via Iran before the development of the Sahara may be more plausible. From the end of the Pliocene until today, the expansion of the Sahara formed an increasingly effective barrier to animal migration (Coryndon & Savage 1973). Thus, two independent range extension events are proposed, most likely between the mid Miocene and beginning of the Pleistocene, during the emergence of clade D and the emergence of the genus *Perenethis* which caused the African-Asian distribution of these clades.

TAXONOMY

Discrimination of morpho-species.—When working on the alpha-taxonomic level of poorly known groups for which only pre-

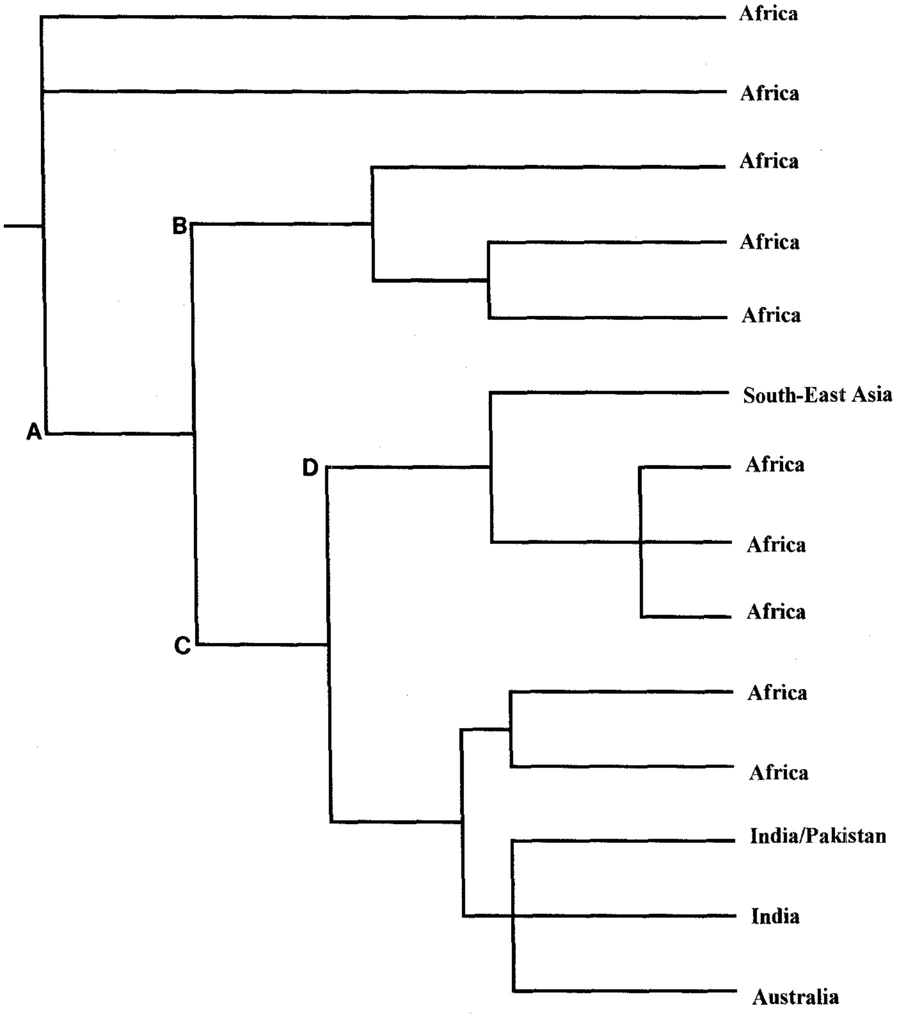


Figure 3.—Area cladogram, taxon names replaced by their distribution.

served material is available, the discrimination of "morpho-species" as a reasonable assessment of biological species becomes the practical solution. In the species revisions of the genera *Perenethis* and *Tetragonophthalma* below, I diverge in some cases quite remarkably from species delimitations drawn by previous authors, mainly Roewer (1955), but also Blandin (1974a—1979b). For this reason it appears to be appropriate to present the rationale for morpho-species delimitations employed in this study. A species-typical trait (= character or character state) should: a) occur consistently in all members of the species, b) be qualitatively discrete (= variation should not show continuous overlap among organisms assigned to different species), and c) preferably show congruence with at least one other such trait. Studies on individual variability within samples and/or populations, whenever feasible, should be considered. In most spider groups, discrete traits in the male palpal organ, e.g., shape of median apophysis or tibial apophysis, are good indicators for the recognition of distinct species. Which structural part of the male palpal organ reveals species-typical attributes varies among closely related spider groups, e.g., at the generic level. The retrolateral tibial apophysis, the median apophysis, the conductor and, within the Pisaurinae, the distal tegular apophysis, are often species-typical.

The female epigynum can show quite a range of variation within a species, which led to numerous redundant species descriptions, e.g., *Thalassius spinosissimus* (Karsch 1878) with its 40 junior synonyms (Sierwald 1987). The ducts and spermathecae of the vulva show less individual variability and are therefore more reliable features for the discrimination of species, at least in all Pisauridae I have examined so far, e.g., the shape of the head of spermathecae in *Thalassius* (see Sierwald 1987). For alpha-taxonomic studies of spiders, the structure of the vulva should always be included if females are available. Within the species studied for the present paper, the duct leading from the head to the base of the spermathecae may show variations in its loops, even differing between the left and right sides of a single individual. Subadult females with heavily sclerotized pre-epigyna (primordia of the developing copulatory organs, Sierwald 1989b) have been mistaken for adults and consequently caused the description of synonymous taxa or *nomina dubia* as in *Maypacius bilineatus* (Pavesi 1895), see Blandin 1975a. Congruence of discrete traits in both male and female copulatory organs permit reliable species-discrimination. Somatic features, such as color-pattern, eye-pattern, spination and leg formula that occur consistently in concordance with discrete traits of copulatory organs of one of both sexes furnish additional species-typical attributes. Somatic features often facilitate recognition of conspecific sexes, but may display sexual dimorphism (see *Tetragonophthalma* below). From my experience with Pisauridae, coloration and color-pattern are prime candidates for sexual dimorphism and polymorphism within species. However, there are noteworthy exceptions such as the color pattern in both sexes of *Perenethis symmetrica* which is consistently different from all other species of the genus.

Taxonomic history of the *Perenethis* genus group.— The *Perenethis* genus group comprises the pisaurine genera *Charminus*, *Cispius*, *Tetragonophthalma*, *Afropisaura*, *Perenethis*, *Maypacius*, and *Polyboea*. The African genera *Charminus* and *Cispius* are morphologically similar and have been confused in the past. Blandin (1978a) separated both genera conclusively by features of the eye pattern, the tibial apophysis and the embolus, and moved several species originally described in *Cispius* to *Charminus*. The genera *Tetragonophthalma*, *Perenethis* and *Maypacius* each have caused taxonomic problems and misinterpretations since their introduction to arachnology (comprehensive review by Blandin 1974a). Several species were shifted mainly among the three genera [e.g., *Maypacius bilineatus*, described *sub Tetragonophthalma*], probably due in part to the homogeneity of certain morphological features (especially the structure of the epigynum) and in part due to misidentification of genus-typical characters (e.g., retromarginal cheliceral teeth). The major event causing confusion was an incorrect re-description of the genus *Tetragonophthalma* by Simon (1898a), in which he cited two retromarginal cheliceral teeth. Karsch (1878), in the original description of *Tetragonophthalma*, did not give the number of teeth at the posterior margin of the chelicerae. Dahl (1908) examined the holotype of *Tetragonophthalma phylla* Karsch 1878 (type species of the genus), noted four cheliceral teeth, and rejected Simon's synonymy of *Perenethis* with *Tetragonophthalma*. Meanwhile, Simon (1898) had introduced the genus *Phalaea* to accommodate species with four teeth at the posterior margin of the chelicerae, thus creating a junior synonym for *Tetragonophthalma*. Subsequent authors either followed Simon's interpretation of the genus *Tetragonophthalma* [e.g., Bösenberg & Strand 1906 in the description of *Perenethis fascigera* under *Tetragonophthalma]* or rejected it (Pocock 1900). Roewer (1955) reviewed the issue and re-examined the immature type of *T. phylla* (which apparently has been lost since; *fide* Blandin 1976a). The genus *Afropisaura* was recently described by Blandin (1976b) for three African species formerly placed in the genus *Pisaura*. The monotypic genus *Polyboea* was introduced by Thorell (1895) for a juvenile male from Burma. Male and female of the type species are figured here for the first time.

Charminus Thorell 1899

Figs. 4, 5, 8–11

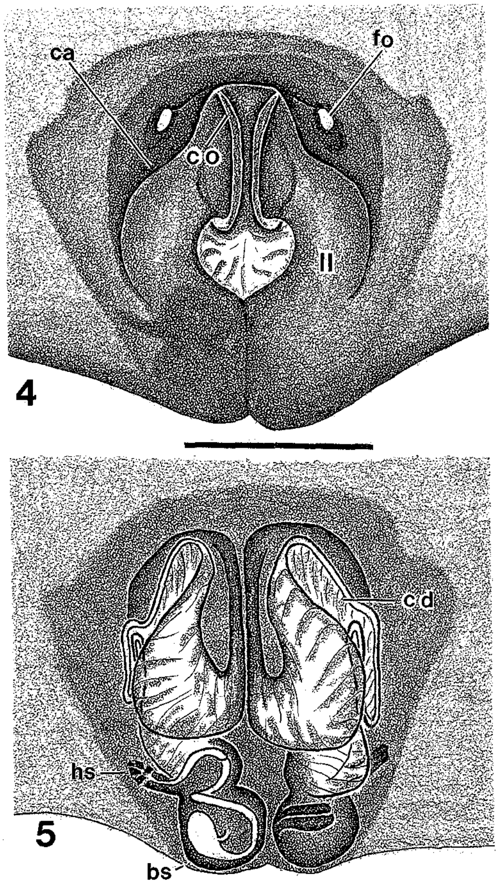
Charminus Thorell 1899: 83. Type species, by original designation, *Charminus camerunensis* Thorell 1899: 83; ♂♀, Cameroon.

Nine species are currently recognized in the genus; two species are known from females only, one is known from a single male. Valid species of the genus: *Charminus aethiopicus*

Caporiacco 1939, ♂♀ known; *Cispius ambiguus* Lessert 1925, ♂♀ known; *Cispius atomarius* Lawrence 1942, ♂♀ known; *Charminus bifidus* Blandin 1978 (1978a), ♂ known; *Charminus camerunensis* Thorell 1899, ♂♀ known; *Cispiolus marfieldi* Roewer 1955, ♂♀ known; *Cispius minor* Lessert 1928, ♂♀ known; *Cispius natalensis* Lawrence 1947, ♀ known; *Charminus rotundus* Blandin 1978 (1978a), ♀ known.

Diagnosis.—AER recurved (*ch* 2), three cheliceral teeth (*ch* 0); epigynal folds anteriorly parallel and close to each other (*ch* 7), carina procurved (*ch* 9); conductor with narrow basal stalk (*ch* 25) and broad, rounded, flaplike apical section (*ch* 24); single guiding fold for embolus (*ch* 27); embolus long and whip like (*ch* 33). Autapomorphic characters: AE nearly same size as PE (*ch* 3), lateral flap at conductor, carina with lateral lobes. Synapomorphic characters: Procurved carina as in *Cispius* (*ch* 9). The membranous saclike copulatory duct forming two loops (*ch* 14) occurs at least in some species of the following pisaurine genera: *Afropisaura*, *Perenethis*, and *Polyboea*; in *Tetragonophthalma*, the two loops are sclerotized (*ch* 13) but their shape and trajectory are identical to *Afropisaura*. The copulatory ducts in other pisaurine genera are different, as far as currently known.

Description of *Charminus camerunensis* Thorell 1899.—(2♂1♀). *Measurements:* ♀ slightly larger than ♂, ♂ with longer legs than ♀. ♀ body 7.8–9.7 long, prosoma 2.8–3.5 long, 2.5–2.9 wide. Leg length: (prosoma 3.5 long) Fe 5.2, PaTi 6.5, MeTa 7.5, total length 19.5. ♂ body 8.7 long, prosoma 3.5 long, 2.7 wide. Leg length: Fe 6.3, PaTi 8, MeTa 9.8; total length 24.1. Eye pattern: AER recurved and only slightly shorter than PER, AE slightly smaller than PE, PME:AME = 1.2; ALE slightly smaller than AME or AME=ALE. Chelicerae: Posterior margin dentition somewhat variable even within individuals, mostly with three, some individuals with four teeth; teeth unequal in size, equally-sized in *Charminus ambiguus*). Spine pattern: See Table 6. Epigynum (Fig. 4): Epigynal folds parallel and close together anteriorly, curved in the middle section, adjoining in the posterior section; entire carina procurved; posterior edge ridgelike, anterior edge indistinct; fossae lateral to copulatory openings. Vulva (Fig. 5): Copulatory duct membranous, two loops, first loop larger than second, head of spermatheca pointing laterally, spermathecal duct with one loop, base of spermatheca bulbous, with small lumen. Male palp (Figs. 8–11; Sierwald 1990, figs. 49–50): Retrolateral tibial apophysis simple, perpendicular, tip pointed; conductor base narrow, apical section broad with genus-typical flap (Blandin 1978a: figs. 22–27) and single low guiding fold; median apophysis with S-shaped hook; distal tegular apophysis with wing and hook; base of dst with two ridges, embolus long, pars pendula ⅓ of embolus length.



Figures 4, 5.—*Charminus camerunensis* from Gabon. 4, Epigynum; 5, Vulva. Scale line = 0.5 mm.

Taxonomic note.—*Charminus aethiopicus* (Caporiacco 1939) NEW COMBINATION. *Cispius novus* Caporiacco 1941 and *Cispius tertali* Caporiacco 1941 are both subjective junior synonyms of *Charminus aethiopicus* (Caporiacco 1939) NEW SYNONYMIES. The male palps of *C. tertali* (♂ holotype) and *C. aethiopicus* (♂ syntypes) are morphologically identical. The female specimens of *Cispius novus* (♀ syntypes) share a unique somatic feature with *Cispius aethiopicus* and *Cispius tertali*: In all specimens, the outermost of the three cheliceral teeth at the retromargin is distinctly smaller than the other two (see cheliceral teeth in *Charminus camerunensis* for comparison). The female specimens of *Cispius novus* were collected at the same locality as the *Cispius tertali* specimen.

Specimens examined.—*Charminus aethiopicus*: **KENYA**: *Moyale*, 2♂ (syntypes), 18 May 1937 (MZUF). *C. ambiguus concolor*: **TANZANIA**: *Arusha*, 1♀, 1905 (HNHM). *Moschi*, 2♀, 1904 (HNHM). *C. ambiguus*: **SOUTH AFRICA**: *Natal*, St. Lucia National Park, Fanies Camp, 28°S, 32°30′E, 1♂2♀, 24 January 1991 (V.D. & B. Roth) (CASC). **MALAWI**: *Mukuwazi*, Hill Forest, 11 mi S of Nkata Bay, 590 m, 1♂, 22 February 1958 (E.S. Ross & R.E. Leech) (CASC). *C. camerunensis*: **CAMEROON**: *Kitta*, 5♂1♀ syntypes (NHRS 1406). **GABON**: *Makokou*, 2♀ (Riechert). *C. minor*: **ZAIRE**: *Faradje III*, 1♀, one of two syntypes [other syntype in MHNG, bocal 38] (AMNH). **NIGERIA**: *Ikeja Airport*, Lagos, 1♀, 19 December 1948 (E.S. Ross & R.E. Leech) (CASC). *C. marfieldi*: **RUANDA**: 40 km E of Kigale, 1575 m, 1♀, 9 December 1957 (E.S. Ross & R.E. Leech) (CASC). *C. natalensis*: **ZAIRE**: 8 mi W of Luanxa, 1330 m, 1♀, 15 January 1958 (E.S. Ross & R.E. Leech) (CASC). *C. novus*: **ETHIOPIA**: *El Banno*, 3♀ (syntypes), 30 April–4 May 1939, Missione Biologica Sagan-Omo (Prof. E. Zavattari) (MZUF). *C. tertali*: **ETHIOPIA**: *El Banno*, 1♂ (holotype), 7 May 1939, Missione Biologica Sagan-Omo (Prof. E. Zavattari) (MZUF).

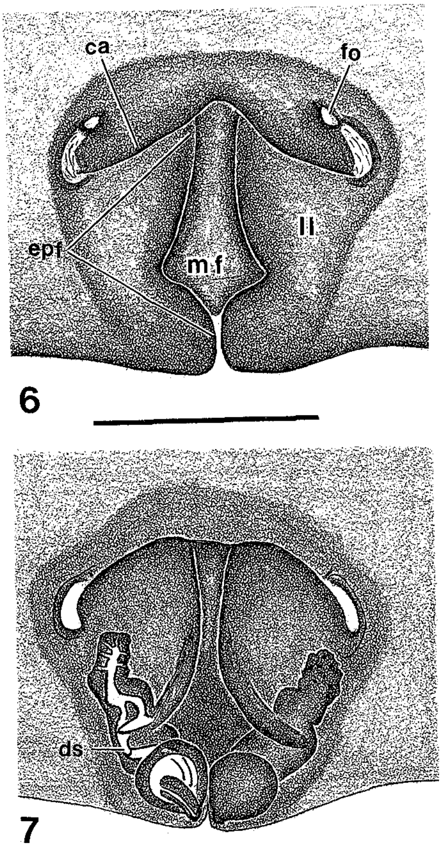
Cispius Simon 1898
Figs. 6, 7, 12–16

Cispius Simon 1898a: 296. Type species, by original designation, *Cispius variegatus* Simon 1898b: 19, ♀, Congo, Landana.

The genus currently contains eight species; four species are known from females only, three from males only. For *Cispius maruanus* both sexes are known (Blandin 1978a). Valid species of genus: *C. affinis* Lessert 1916, ♀ known; *C. bidentatus* Lessert 1936, ♂ known; *C. kimbius* Blandin 1978 (1978a), ♀ known; *Nilus maruanus* Roewer 1955, ♂♀ known; *C. problematicus* Blandin 1978 (1978a), ♂ known; *C. simoni* Lessert 1915, ♀ known; *C. thorelli* Blandin 1978 (1978a), ♂ known; *C. variegatus* Simon 1898 (1898b), ♀ known.

Diagnosis.—AE distinctly smaller than PE (*ch* 3), AER recurved (*ch* 2), three cheliceral teeth in most species (*ch* 0), epigynal folds anteriorly parallel and close to each other (*ch* 7), carina procurved (*ch* 9); conductor broad, rounded, flaplike (*ch* 22–25). Autapomorphic characters: Male retrolateral tibial apophysis large, broad and perpendicular; distal tegular apophysis large, with smoothly rounded apical margin, shape unique; distal sclerotized tube of embolic division large (*ch* 32), tip reaches tip of embolus, additional sclerite of species-typical size within pars pendula (*ch* 34), embolus short but massive (*ch* 33). Synapomorphic characters: Procurved carina as in *Charminus* (*ch* 9).

Description of species.—Measurements: *C. variegatus*, 3♀: Prosoma 2.4–2.9 long, 2.0–2.4 wide, body 5.0–7.1 long (MRAC 12.320/22). *C. thorelli*, 2♂ holotype, paratype: Prosoma 3.5—4.2 long, 2.9–3.4 wide, body 6.5–7.5 long (MRAC 121.176; 148.599). *C. bidentatus* ♂ holotype: Prosoma 6.9 long, 4.2 wide, body 11 long (MHNG, boc 38); ♂ prosoma 3.8 long, 3 wide, body 8 (MRAC 145. 399). Eye pattern: AER recurved (sometimes almost straight) and only slightly shorter than PER, AE distinctly smaller than PE, PME:AME = 1.4; AME:ALE = 1.3. Chelicerae: *C. thorelli*, *C. variegatus*, and *C. problematicus*: Three teeth at posterior margin of chelicerae, outermost slightly smaller, *C. bidentatus* with only two (specimen from Tanzania with three cheliceral teeth); teeth unequal in size. Spine pattern and spine length: As in *Charminus*. Epigynum (*C. variegatus*, Fig. 6): Epigynal folds anteriorly parallel, small distance apart; entire carina procurved, posterior edge ridgelike, anterior edge weakly developed; fossae lateral to copulatory openings. Vulva (Fig. 7): Copulatory duct sclerotized, short and curved; large head of spermatheca pointing anteriorly, spermathecal duct with one loop, base of spermatheca large and bulbous with large lumen. Male palp (*C. thorelli*, Figs. 12–14): Retrolateral tibial apophysis large and perpendicular to tibia; conductor large with rounded tip; median apophysis slender with S-shaped hook; distal tegular apophysis with large, rounded tip; sclerite *A* similar to *Charminus*, distal tegular apophysis large, reaches tip of embolus; em-



Figures 6, 7.—*Cispius variegatus* from Zaire (MRAC 12.320). 6, Epigynum; 7, Vulva. Scale line = 0.5 mm.

bolus moderately long, but massive, pars pendula reaches tip of embolus; sclerite within pars pendula may represent truncus. *C. problematicus* (♀ unknown): ♂ with uniquely large sclerite *A* (see Blandin 1978a: fig. 21) and with two pointed sclerites visible at tip of the embolus as in *C. bidentatus*.

Taxonomic notes.—The species *Cispius orientalis* described by Yaginuma (1967) has been placed in a new genus *Shinobius* Yaginuma 1991. It has no affinities to the Pisaurinae, but to the Rhoicininae (Sierwald 1993). The types of *C. delesserti* Caporiacco 1947, *C. kovacsi* Caporiacco 1947, and *C. strandi* Caporiacco 1947, cannot be located in the Museum in Budapest, Hungary (Mahunka *in litt.* 1986).

Specimens examined.—*C. bidentatus*: **MOZAMBIQUE**: *Vila Pery* , ♂ holotype (P. Lesne) (MHNG, bocal 38). **KENYA**: *Diani Beach*, 1♂, May 1957 (N.L.H. Kraus) (AMNH). **ZAIRE**: *Albertville*, Verhonstraete, 1♂, 1960 (MRAC 145.399). **TANZANIA**: 10 mi SE of Amani, 160 m, 1♂, 11 November 1957 (E.S. Ross & R.E. Leech) (CASC). *C. kimbius*: **SOUTH AFRICA**: *Natal*, St. Lucia National Park, collected from hole in tree bark, Fanies Camp, 28°S, 32°30'E, 3♀, 24 January 1991 (V.D. & B. Roth) (CASC). *C. thorelli*: **ZAIRE**: *Katanga*, Elisabethville, ♂ holotype, January 1962 (M. Lips) (MRAC 121.176). Albertville, Verhonstraete, ♂ paratype, 1960 (MRAC 148.599). *C. problematicus*: **SOUTH AFRICA**: *East Transvaal*, 15 km from Klaserie, woodland, Guernsey Farm, 2♂, 18–31 December 1985 (S. & J. Peck) (AMNH). *East Transvaal*, stream side thorn scrub, Kruger Park, Satara, 1♂, 15–18 December 1985 (S. & J. Peck) (AMNH). *C. variegatus*: **ZAIRE**: *Komi*, Lodja, 3♀, January-February 1930 (MRAC 12.320-12.322).

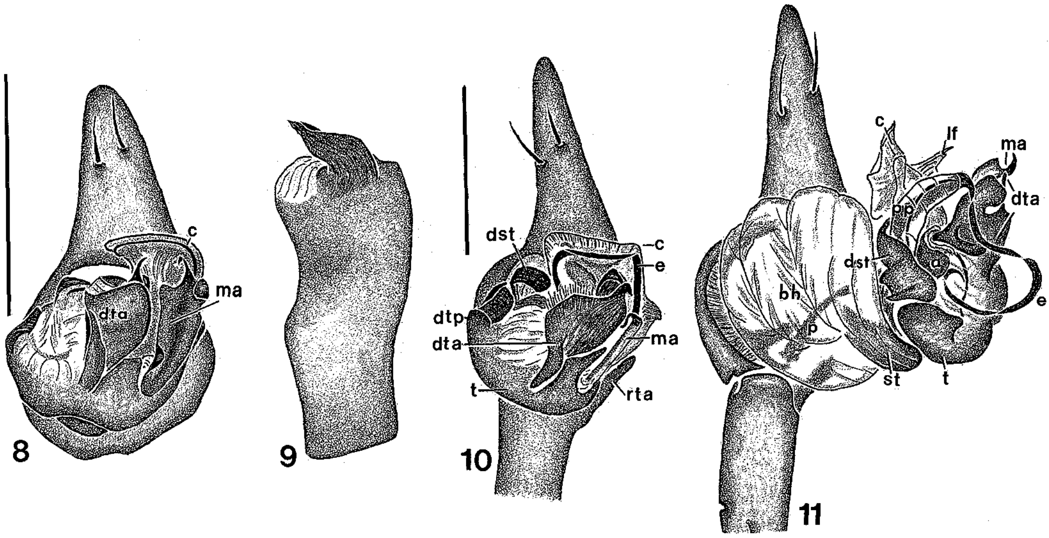
Afropisaura Blandin 1976
Figs. 17–22, 25, 26

Afropisaura Blandin 1976b: 926. Type species, by original designation, *Pisaura valida* Simon 1885: 354 (♀), Senegal, Dakar.

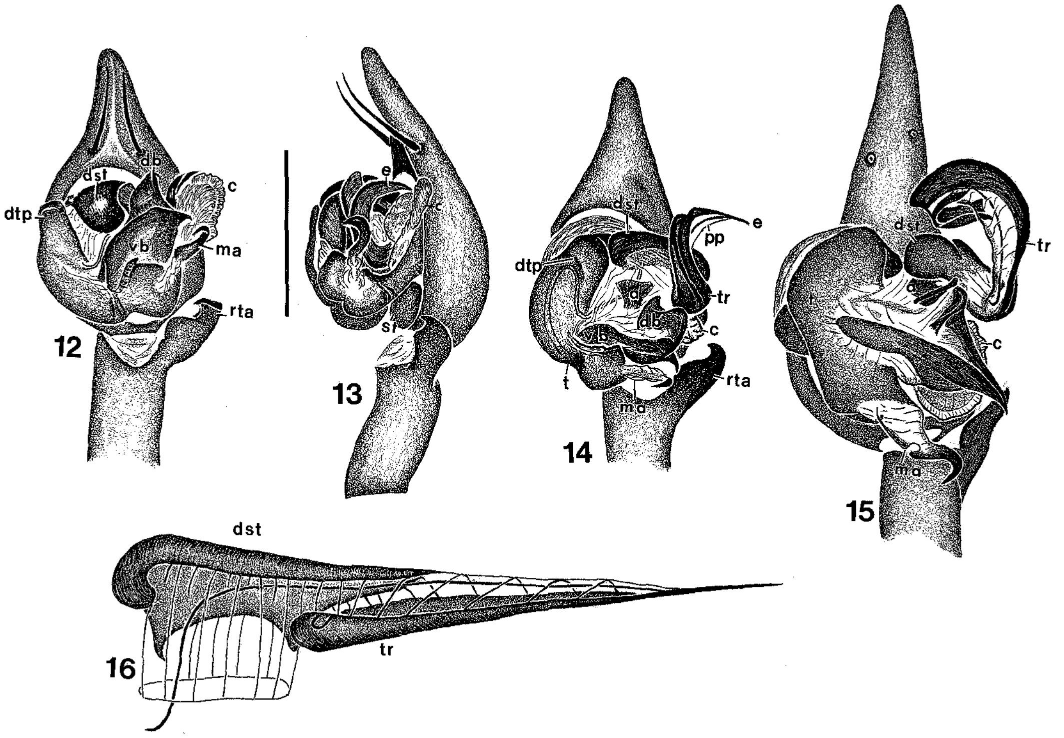
Blandin (1976b) included *A. valida*, *A. rothiformis* (Strand 1908) and *A. ducis* (Strand 1913) in his newly described genus *Afropisaura* and placed *Pisaura camerunensis* Roewer 1955 in the synonymy of *A. ducis*. Both sexes are known for the three species.

Diagnosis.—AER straight or slightly procurved (*ch* 2), ALE≥AME (*ch* 4); three equally-sized cheliceral teeth (*ch* 0), posterior section of copulatory duct of vulva with several, partly sclerotized undulations (*ch* 13). Autapomorphic characters: Truncus attached to distal sclerotized tube of embolic division, forming an angle; large median apophysis with blade-shaped tip; short conductor with broad base, tapering apically (*ch* 22). Central excavation opening posteriorly under lip-like carina. Vulva: Anterior section of copulatory duct sclerotized (*ch* 13). Synapomorphic characters: Liplike carina (*ch* 10), sclerotized anterior section of copulatory duct, and posterior section of copulatory duct undulated as in *Tetragonophthalma* (*ch* 13).

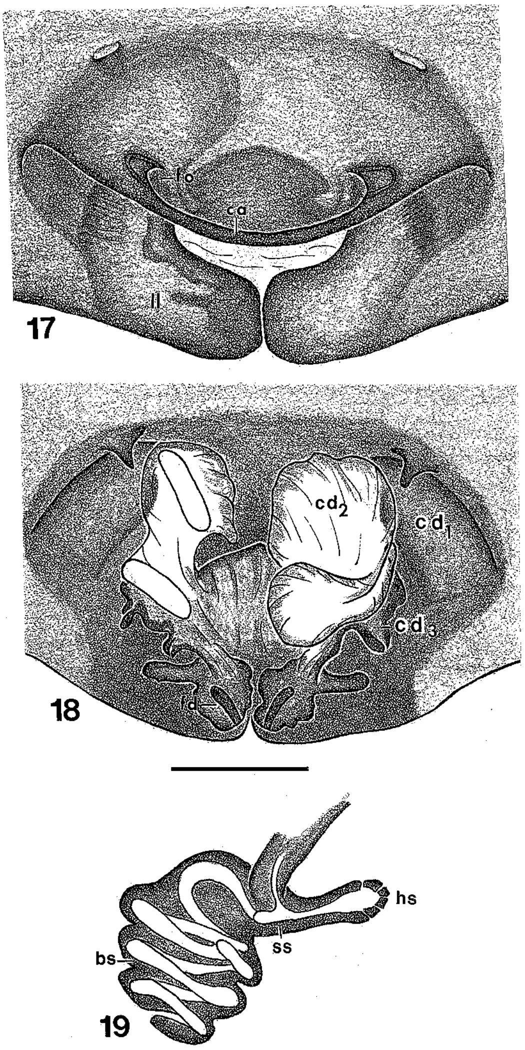
Description of *A. valida* and *A. ducis*.—Measurements: *A. ducis*: Both sexes of same size, males with longer legs than females. Female range from body 9.75 long [prosoma 3.5 long, 3.0 wide (SMFD RII/7930/52)] to body 13.49 long [prosoma 5.16 long, 4.33 wide (SMFD RII/10008)]. Male range from body 11.6 long [prosoma 4.58 long, 3.70 wide (ho-



Figures 8–11.—*Charminus*, left male palp. 8, 9, *Charminus aethiopicus* from Kenya (syntype; MZUF). 8, Unexpanded palp, ventral view; 9, retrolateral tibial apophysis. Scale line = 0.5 mm. 10, 11, *Charminus camerunensis* from Cameroon (syntype; NHRS, 1406). 10, Unexpanded palp, ventral view; 11, Expanded palp, prolateral view. Scale line = 0.5 mm.

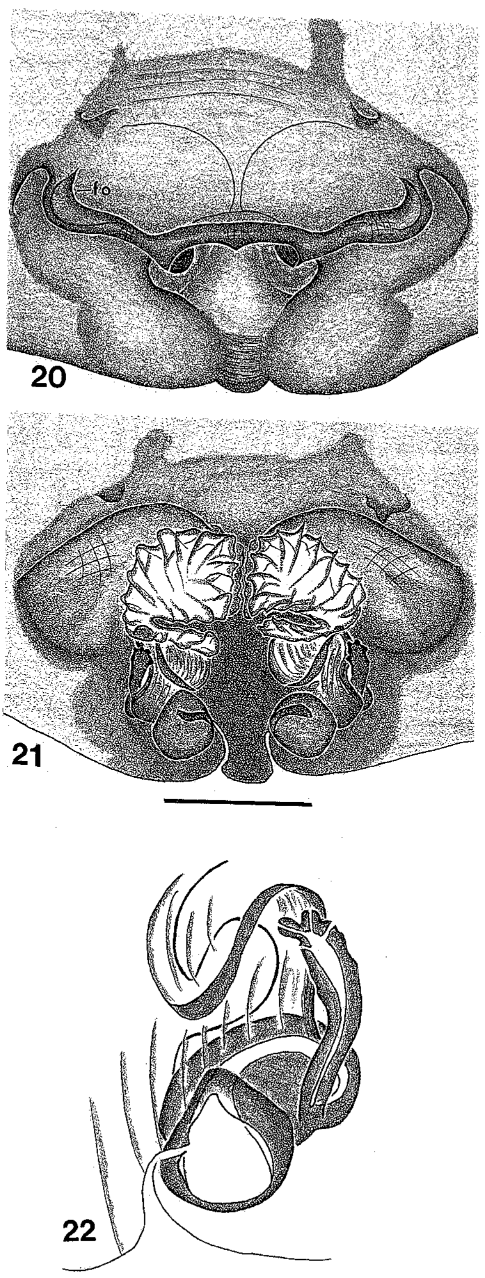


Figures 12–16.—*Cispius*, left male palp. 12–14, *Cispius thorelli* from Zaire (MRAC 148.599). 12, Unexpanded palp, ventral view; 13, Unexpanded palp, retrolateral view; 14, Expanded palp, ventral view (MRAC 148.599). 15, 16, *Cispius bidentatus* from Zaire (MRAC 145.399). 15, Expanded palp, ventral view; 16, Embolus sclerites, schematic. Scale line = 0.5 mm.



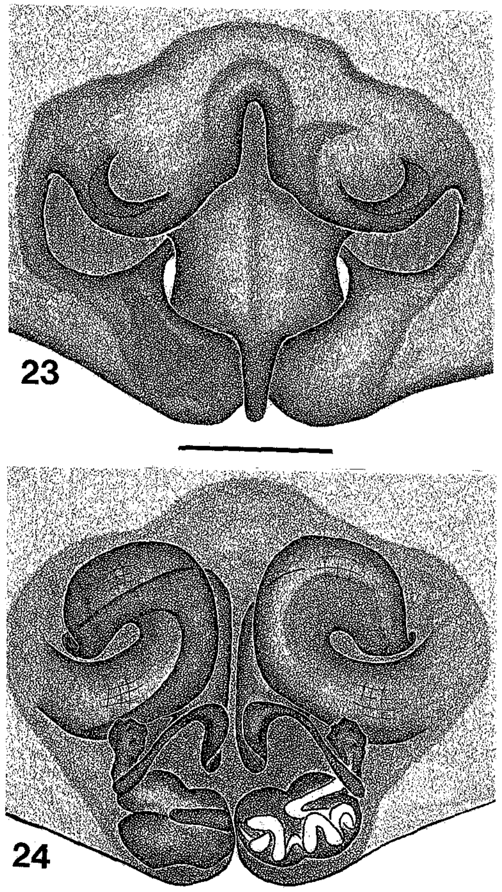
Figures 17–19.—*Afropisaura valida* from Congo (MRAC 29.531). 17, Epigynum; 18, Vulva; 19, Left spermatheca, dorsal view. Scale line: 17, 18 = 0.5 mm; 19 = 0.2 mm.

lotype *ducis*)] to body 13.1 long [prosoma 5.2 long, 4.16 wide (SMFD RII/10329/79)]. *A. valida*: ♀ range from body 9.3 long [prosoma 4.16 long, 3.66 wide (MRAC 29 528-31)] to body 17 long [prosoma 7.08 long, 6.25 wide (lectotype, MNHN 4922)]. Leg length: (prosoma 4.16 long) Fe 4.41, PaTi 5.6, MeTa 5.41; total length 15.42. Male range from body 11.26 long [prosoma 4.66 long, 3.83 wide (MRAC 29647)] to body 12.88 long [prosoma 5.8 long, 4.5 wide (MNHN "néallotype")]. Leg length (prosoma 4.66 long) Fe 5.83, PaTi 7.5, MeTa 7.16; total length 20.5. Eye pattern:



Figures 20–22.—*Afropisaura ducis* from Zaire (SMF RII/10008). 20, Epigynum; 21, Vulva; 22, Left spermatheca, dorsal view. Scale line: 20, 21 = 0.5 mm; 22 = 0.2 mm.

AER: Straight in *A. valida*, procurved in *A. ducis*; PME>PLE=ALE≥AME (*ch* 3,4), *A. valida*: PME:AME = 1.2, AME=ALE; *A. ducis*: PME:AME = 1.6, AME:ALE = 0.7; in *A. ducis* and *A. rothiformis* AME conspicuously smaller (Blandin 1976b, figs. 4, 19, 20)

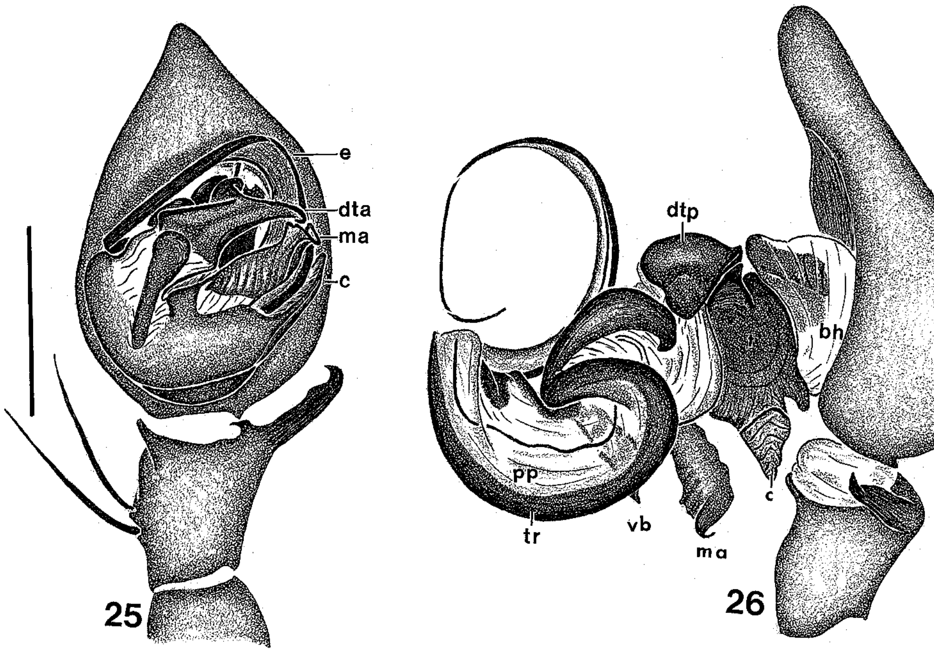


Figures 23, 24.—*Tetragonophthalma vulpina* from Zaire (MRAC 12.668). 23, Epigynum; 24, Vulva. Scale line = 0.5 mm.

than in *A. valida*. Chelicerae: Posterior margin with three equally-sized teeth, equally spaced. Spine pattern (Table 6): Patella with a thin dorsal proximal spine and two lateral spines. Spine length [ventral tibial spine, second pair, first leg]: Spine length:tibia width = 3. Epigynum (Figs. 17, 20): Rather large in all three species; epigynal folds form a V; fossae above copulatory openings and in *A. valida* closer together than in *A. ducis*; deep pit under median section of carina opening posteriorly; copulatory openings in *A. valida* considerably larger than in *A. ducis*. Vulva (Figs. 18, 19, 21, 22): Copulatory duct divided in three sections; anterior section (cd1) sclerotized with large lumen; middle section (cd2) membranous saccate tube, forms two loops of unequal size; posterior section (cd3) narrow fold with sclerotized edge; head of spermatheca of moderate size, pores conspicuous; position of head of spermatheca appears to be variable within *A. ducis* pointing anteriorly or posteriorly (type of *Pisaura camerunensis* [= *A. ducis*]: Head of spermatheca seems to point posteriorly, visible through body wall); *A. valida*—specimen examined: Head of spermatheca points laterally. *A. valida* (Fig. 19): Spermathecal duct with four loops; base of spermatheca without lumen. *A. ducis* (Fig. 22): Spermathecal duct forms single curve, base of spermatheca with large lumen. Male palp (Figs. 25, 26, based on *A. valida* and *A. ducis*, Blandin 1976b, fig. 26): Tegulum platelike and strongly sclerotized on both sides; conductor stiff, sclerotized, with broad base and pointed tip, considerably shorter than in all other Pisaurinae; prolateral wall of conductor membranous and inflatable; median apophysis flat with bladelike tip, pointing retrolaterally; distal tegular apophysis large, with club-shaped base, ventral branch ends in pointed hook. Sclerite *A* well developed with two prongs pointing dorsally in *A. valida*, simple saber-shaped in *A. ducis* (not visible in unexpanded palps). Distal sclerotized tube of embolic division large; truncus of embolus arises at its distal tip and runs backwards, thus forming a sharp angle (called "protuberance" by Blandin). Broad pars pendula follows truncus about ¾ of embolus length; concave edge of pars pendula sclerotized, especially proximately.

Natural history.—Females of *Afropisaura* valida construct a nursery web (Blandin 1979b).

Specimens examined.—*A. ducis*: **ZAIRE**: *Kivu Province*, Lake Kivu, ♂ holotype, (ZMHB 28 356). **TANZANIA**: *Arusha*, ♀ "allotype" 2♂ (SMFD RII/10329/79). **ZAIRE**: *Upemba Nat. Park*, 1♂1♀ (SMFD RII/10008). **CAMEROON**: *Yaoundé*, 1♀ (holotype *Pisaura camerunensis*) (SMFD RII/7930/52). *A. rothiformis*: **NIGERIA:** *Abarka (Kwale) Warri*, 1♀, 2 January 1949 (B. Malkin) (CASC). **CAMEROON**: *Mkuyka*, Victoria Div., 1♂, 24–29 June 1949 (B. Malkin) (CASC). **ANGOLA**: *Lunda Province*, Dundo, 1♀, 21 September 1949 (B. Malkin) (CASC). *A. valida*: **CONGO**: 1♂2♀, (MRAC 29.528-29.531). 1♂ (MRAC 29.647). **IVORY COAST**: *Lamto*, ♂ "néallotype" (MNHN). **SENEGAL**, ♀ lectotype (designated by Blandin) 2 juv. (MNHN 4.922). **ANGOLA**: *Lunda Province*, Dundo, 1♂, 21 September 1949 (B. Malkin) (CASC).



Figures 25, 26.—*Afropisaura valida*, left male palp from Congo (MRAC 29.647). 25, Unexpanded, ventral view; 26, Expanded, retrolateral view. Scale line = 1 mm.

Tetragonophthalma Karsch 1878
Figs. 23, 24, 27–30

Tetragonophthalma Karsch 1878: 329. Type species, by monotypy, *Tetragonophthalma phylla* Karsch 1878: 329; ♀ juvenile; Ghana, Accra. Immature female type specimen, apparently lost (*fide* Blandin 1976a: 588). Considered a *nomen dubium* by Blandin (1976a: 588).

Blandin (1976a) recognized eight valid species in the genus, placed *T. ferox* (Pocock 1899) in the synonymy of *T. crassa* (Thorell 1899), and listed five *nomina dubia*. Types of every available African species of the genus *Tetragonophthalma* (9♂12♀) were examined for the present study. All eight species are here considered to be conspecific. No concordant differences were found in the males examined. The female epigynum displays a moderate range of variation, but the vulvae display only minor variability. The body-length variation of adult females is high. Therefore, the nominal species *T. balsaci*, *Phalaea crassa*, *Phalaea ferox*, *T. guentheri*, *T. lecordieri*, *T. pelengea*, *Phalaea thomensis*, and *T. wittei* are here regarded as subjective junior synonyms of *Tetragonophthalma vulpina* (Simon 1898). *Diapontia freiburgensis* Keyserling 1877 (1877: 671), transferred to *Tetragonophthalma* by Keyserling (1891: 255), and *Tetragonophthalma obscura* Keyserling 1891 (1891: 256), the only South American species ever associated with one of the pisaurine genera as here defined, were transferred to *Porrimosa* Roewer 1960, family Lycosidae, by Capocasale (1982: 146).

Tetragonophthalma vulpina (Simon 1898)

Phalaea vulpina Simon 1898b: 14 (♂♀).

Phalaea crassa Thorell 1899: 80 (♀) NEW SYNONYMY.

Phalaea ferox Pocock 1899: 863 (♀); considered a subjective junior synonym of *crassa* by Blandin (1976a: 592) NEW SYNONYMY.

Phalaea thomensis Simon 1909: 386 (♀) NEW SYNONYMY.

T. guentheri Roewer 1955: 172 (♀) NEW SYNONYMY.

T. pelengea Roewer 1955: 179 (♂♀) NEW SYNONYMY.

T. wittei Roewer 1955: 181 (♂♀) NEW SYNONYMY.

T. lecordieri Blandin 1976a: 601 (♂♀) NEW SYNONYMY.

T. balsaci Blandin 1976a: 602 (♂♀) NEW SYNONYMY.

Diagnosis.—Large spiders (♀ up to 40 mm long) with the following autapomorphic char-

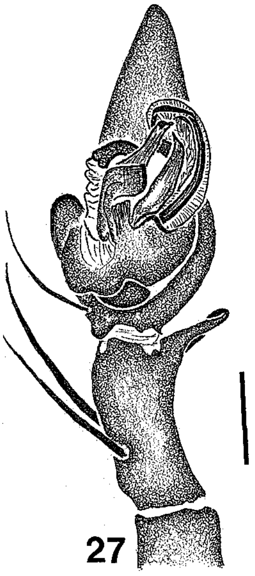
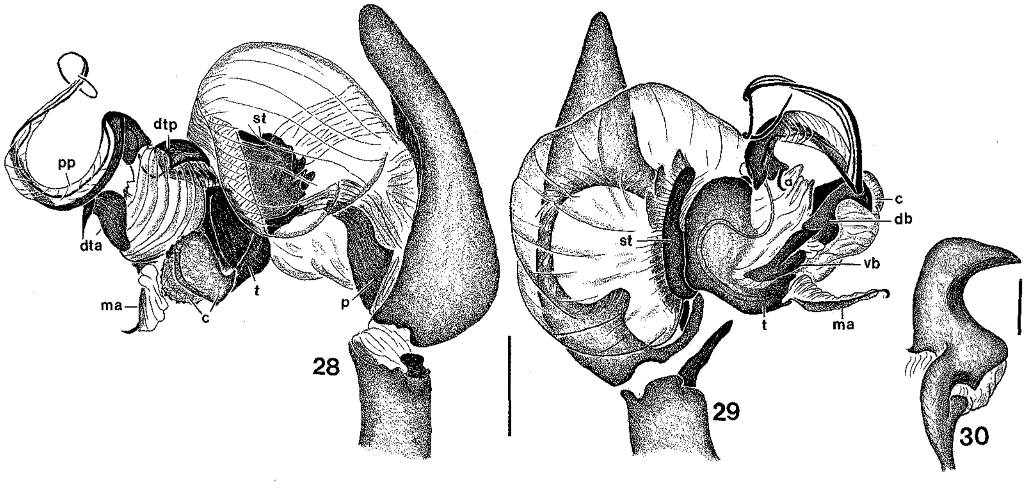


Figure 27.—*Tetragonophthalma vulpina*, left male palp, unexpanded, ventral view; (paratype of *T. lecordieri*; MRAC 123.720). Scale line = 1 mm.

acters: AER strongly procurved (*ch* 2); four cheliceral equally-sized teeth (*ch* 0, 1); sexual dimorphism in spination of patella and tibia unique within the Pisaurinae (*ch* 5); spines short (*ch* 6); carina continuous, with deep median notch; copulatory duct fully sclerotized (*ch* 13); hook at distal tegular apophysis in male bulb large. Synapomorphic characters: Liplike carina (*ch* 10), sclerotized anterior section of copulatory duct and undulated posterior copulatory duct shared with *Afropisaura* (*ch* 13).

Description of *T. vulpina*.—Measurements: Females are larger than males, males have relatively longer legs than females. Female body range from 16.1 long (prosoma 6.8 long, 5.2 wide [holotype of *P. thomensis*]) to 40 long (prosoma 16 long, 11.4 wide [holotype of *P. crassa*]). Leg length: Female (prosoma 8.4 long, holotype of *T. lecordieri*) Fe 13.5, PaTi 18.3, MeTa 22; total length 53.8. Male body range from 16.7 long (prosoma 6.2 long, 5 wide [paratype of *T. lecordieri]*) to 24.5 long (prosoma 10 long, 8.4 wide [paratype of *T. pelengea*, MRAC 119.706]). Leg length (prosoma 8.2 long, [paratype of *T. pelengea*, MRAC 119.706]) Fe 17, PaTi 22, MeTa 24; total length 63. Eye pattern: AER strongly procurved; anterior lateral eyes on tubercles of variable size; PLE > PME = ALE > AME (*ch* 3,4); PME:AME = 1.1–1.48. AME:ALE = 0.7–0.9. Variability in eye-sizes reflects variability in body-size. Chelicerae: Posterior margin typically with four equally-sized teeth. Variation: Less than four teeth on one chelicera or small additional tooth or teeth of different sizes, e.g., *P. thomensis*: Right chelicera 3, left chelicera 4. Spine pattern (see Table 6): Patella spination on legs I and II differs from patella spination on legs III and



Figures 28–30.—*Tetragonophthalma vulpina*, expanded left male palp. 28, 29, Ivory Coast (paratype of *T. lecordieri*; MRAC 123.720); 30, Congo (paratype of *T. balsaci*, MNHN, Simon coll 8536). 28, Expanded, retrolateral view; note expanded conductor; 29, Expanded, ventral view; 30, Hook at distal tegular apophysis, prolateral view. Scale line: 28, 29 = 1 mm; 30 = 0.2 mm.

IV. Sexual dimorphism in dorsal spination of tibia I and II. Spine length: Short [ventral tibial spine, second pair, first leg]: Spine length: tibia width = 1.5. Epigynum (Fig. 23): Epigynal folds anteriorly divergent, middle section straight and far apart, posterior section adjoining; carina continuous, unique shape, forming two flaps over copulatory openings; fossae approximately above copulatory openings. Vulva (Fig. 24): Copulatory duct entirely sclerotized, with two wide loops and a narrow posterior section; head of spermatheca pointing anteriorly, spermathecal duct with five loops, base of spermatheca without lumen. Male palp (Figs. 27–30): Retrolateral tibial apophysis simple, perpendicular to palpal tibia; conductor large, tip broad with low guiding fold; median apophysis slender with hook; distal tegular apophysis with hook, without wing; sclerite *A* small, rod-shaped; embolus moderately long, pars pendula over ⅔ of embolus.

Natural history.—Pocock (1899) mentioned a collector's description of a "*Tetragonophthalma phylla*" web. That description fits the figure given by Blandin (Blandin & Celerier 1981) for webs of the genus *Euprosthenops*. Blandin (1976a) collected *Tetragonophthalma* in wooded habitats. According to my own observations (1980, South Africa, Natal, Hluhluwe) *Tetragonophthalma* lives arboreally and does not build webs.

Specimens examined.—**CONGO**: ♂ paratype of *T. balsaci*, (ES 8536) [*ex* syntype of *T. vulpina*] (MNHN). **CAMEROON**: ♀ holotype of *T. crassa* (Sjöstedt leg. 1891) (NHRS 1403). **EQUATORIAL GUINEA**: *Benito-River*, ♀ holotype of *T. ferox* (BMNH 1898.5.5 101-102) (part). Blandin (1976a: 592) noted three syntypes of *ferox*; Pocock (1899: 863) described ♀ (♀ holotype in BMNH). **TOGO**: ♀ holotype of *T. guentheri* [Parts of ♀ holotype mounted on microscope slides, vial contains remaining parts of holotype and another adult ♀] (ZMHB 13832). **IVORY COAST**: *Lamto*, ♀ holotype of *T. lecordieri* (ENS) (MNHN); *Lamto*, ♀ paratype [cited in Blandin (1976a) with incorrect collection number] (MRAC 134.609); *Bingerville*, ♂ paratype (MRAC 123.720). **ZAIRE**: *Luebo*, ♀ [marked on vial as paratype, not listed as paratype in Blandin 1976a] (MRAC 12.668). **ISL. S. THOMÉ**: *Ribera Palma*, ♀ holotype of *T. thomensis* (MCSN). **ZAIRE**: *Gorges de la Pelenge*, Upemba National Park, ♀ holotype of *T. pelengea* (MRAC 119.705); 2 ♂ paratypes (MRAC 119.706). *T. phylla* (det. Pocock): **SIERRA LEONE**: 1♂1♀ (BMNH 1898.5.5.95-100). **CONGO**: ♀ holotype of *T. vulpina*, (ES. 8536) (MNHN). **GABON**: 1♂ (AMNH). **ZAIRE**: *Mabwe*, Upemba National Park, ♂ holotype of *T. wittei* (MRAC 119.707); ♀ paratype (MRAC 119.708).

Perenethis L. Koch 1878

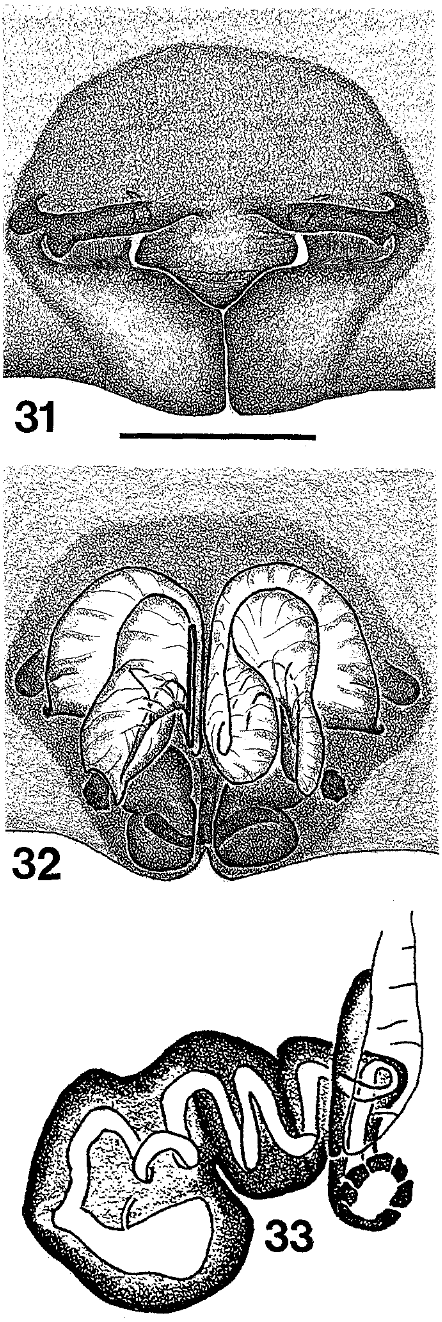
Figs. 31–81

Perenethis L. Koch 1878: 980. Type species, by monotypy, *Perenethis venusta* L. Koch 1878: 980 (♀), Australia, Rockhampton.

Blandin (1975a) recognized four African species. For the present study, all available type material of African and Asian species was examined. Here, two African species (*P. simoni* and *P. symmetrica*), three Asian species, (*P. dentifasciata*, *P. fascigera*, and *P. sindica*), and one Australian species (*P. venusta*) are recognized. *Perenethis huberti* Blandin 1975 and *P. lejeuni* Blandin 1975 are considered subjective junior synonyms of *P. symmetrica* (see Sierwald 1989a).

Diagnosis.—Two cheliceral teeth (*ch* 0), AER slightly procurved (*ch* 2), copulatory duct membranous and saccate (*ch* 13), forming two loops (*ch* 14), of which the first is wider than the second (*ch* 15), conductor with narrow base (*ch* 25), tegulum with basal protuberance (*ch* 21). Autapomorphic characters: Male palp with ventral tibial apophysis (*vta*, *ch* 20); conductor with small mesal hump (*ch* 26) and slender apical section with smoothly rounded tip (*ch* 24); carina forming two lateral branches (*ch* 8). Synapomorphic characters: Two cheliceral teeth at retromargin (*ch* 0) and tegulum with basal protuberance shared with *Polyboea* and *Maypacius* (*ch* 21).

Description of characters.—Eye pattern: AER mostly procurved in varying degrees; eyes rather small and subequal, PLE = PME > AME > ALE, PME:AME = 1.2; AME: ALE = 1.2. Chelicerae: Posterior margin with two unequally-sized teeth close to the inner part of the chelicerae. Color pattern: Median yellowish-brown, rarely red-brown; dorsal pattern with light lateral stripes along prosoma and opisthosoma enclose darker median sections; ventral pattern with grayish coloration of legs (especially femora), dark spots on coxae, grayish patches on sternum. Spine pattern: Legs as in *Charminus*, some specimens with thin, short pro- and retrolateral spines at the patella. Palpal femora with thin ventral spines, feature unusual in the Pisaurinae. Spine length



Figures 31–33.—*Perenethis simoni* from Ivory Coast (MNHN). 31, Epigynum; 32, Vulva; 33, Left spermatheca, dorsal view. Scale line: 31, 32 = 0.5 mm; 33 = 0.2 mm.

[ventral tibial spine, second pair, first leg]: Spine length:tibia width = 3. Epigynum (Fig. 31): Epigynal folds V-shaped, carina ridge-like, straight (except in *P. symmetrica*), forming two separate lateral branches; fossae located in the most lateral corners of the carina branches, lateral in relation to copulatory openings. Vulva (Fig. 32): Copulatory duct saccate and membranous forming two large loops, head of spermatheca bent except in *P. dentifasciata*, spermathecal duct with 3–6 loops, base of spermatheca with small or large lumen. Male palp (Figs. 54–81): Tibia with ventral apophysis; retrolateral tibial apophysis simple and flat, of various lengths, directed forward; tegulum with distinct basal protuberance; weakly sclerotized conductor with narrow base, distinct mesal hump (especially when inflated) and slender apical section with smoothly rounded tip; median apophysis with sclerotized hook; distal tegular apophysis with wing; sclerite *A* small, oval, elongated; distal sclerotized tube of embolic division short and small, consisting mainly of base; embolus long and whip-shaped, pars pendula about ⅔ of embolus length (except *P. symmetrica*).

Natural history.—Koh (1989) collected *P. venusta* in Singapore in "grassy areas"; label indicates collecting with sweep-net. Blandin (1975a) collected *P. simoni* among herbaceous plants. Web-building unknown.

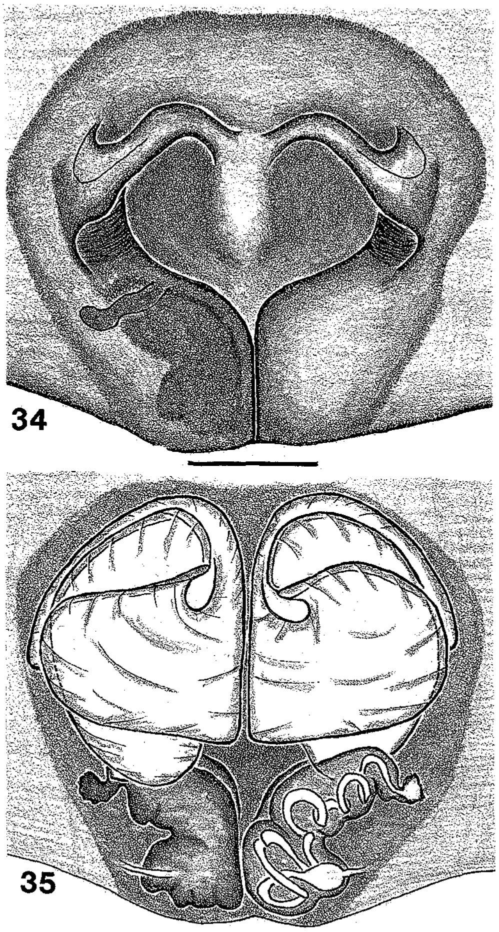
REVISION OF THE GENUS *PERENETHIS*

Perenethis dentifasciata (O. Pickard-Cambridge 1885)
Figs. 48–50

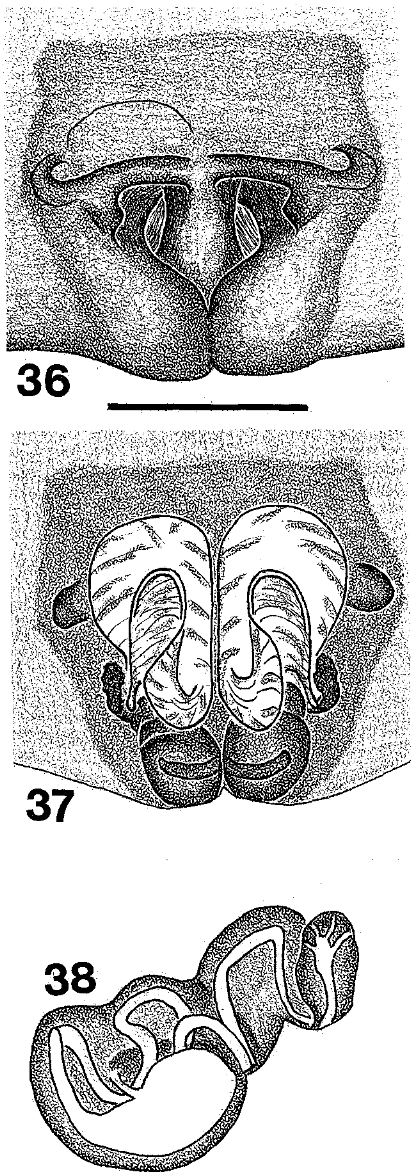
Ocyale dentifasciata O. Pickard-Cambridge 1885: 79; female holotype; type locality: North-east PAKISTAN or north-west INDIA ("Murree to Sind valley, and Sind valley"); OXUM; *vidi*.
Pisaura dentifasciata, –Simon 1898a: 289.
Perenethis dentifasciata, –Sierwald 1987a: 97.
Catalogs: Roewer 1954, 2a: 121, *sub Pisaura*. Bonnet 1955, 2: 3674, *sub Pisaura*. Platnick 1993: 520, *sub Perenethis*.

Diagnosis.—Carina branches very short, unique within *Perenethis* (Fig. 48).

Description (only ♀ holotype known).—Body, legs and palps light yellowish-brown; color pattern faded, most hairs lost; remnants of standard dorsal color pattern similar to *P. simoni* and *P. venusta* (Figs. 52, 53). Measurements: Body 10.6 long, prosoma 3.8 long, 3.25 wide. Leg length: Fe 4.66, PaTi 6.33, MeTa 6.75, total length 17.74. Epigynum (Fig. 48): Central transverse section of carina completely reduced, carina ridges only present around lateral epigynal pits. Vulva (Figs. 49,



Figures 34, 35.—*Perenethis symmetrica* from Djibouti (holotype of *Perenethis huberti*; MNHN). 34, Epigynum; 35, Vulva. Scale line = 0.2 mm.



Figures 36–38.—*Perenethis sindica* from Nepal (CM 267, Mechi District, Taplejung). 36, Epigynum; 37, Vulva; 38, Left spermatheca, dorsal view. Scale line: 36, 37 = 0.5 mm; 38 = 0.2 mm.

50): Copulatory duct saccate and membranous with two loops, first loop considerably wider; small head of spermatheca pointing anteriorly; spermathecal duct with three loops; base of spermatheca ball-shaped with large lumen. Male unknown, see under "Special Forms" for a possible male.

Distribution.—Known only from type locality.

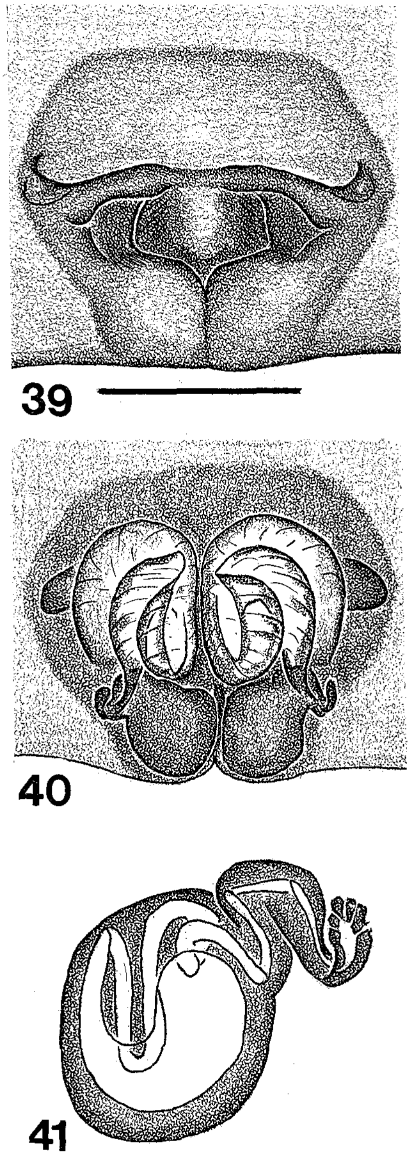
Perenethis fascigera (Bösenberg & Strand 1906)

Tetragonophthalma fascigera Bösenberg & Strand 1906: 306; female holotype; type locality: Japan; Naturkunde-Museum Stuttgart; *non vidi* (holotype lost).

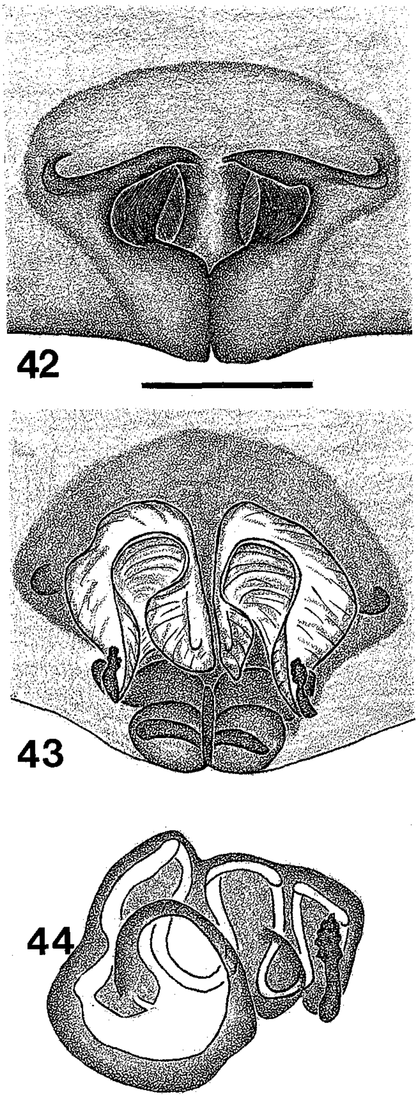
Perenethis fascigera, -Hu 1984: 260. Yaginuma 1986: 173 (♂♀). Song 1987: 209. Chikuni 1989: 106. Chen & Gao 1990: 136. Chen & Zhang 1991: 225.

Catalogs: Roewer 1954, 2a: 118. Bonnet 1955, 2: 4360, *sub Tetragonophthalma*. Platnick 1989: 394, *sub Perenethis*; Platnick 1993: 520.

Description.—Single ♂ and single ♀ from Japan). *Female*: Body, legs and palps yellowish-brown, dorsal color pattern as in *P. venusta* (Fig. 53). Measurements: Body



Figures 39–41.—*Perenethis sindica* from Sri Lanka (OXUM bottle 1526). 39, Epigynym; 40, Vulva; 41, Left spermatheca, dorsal view. Scale line: 39, 40 = 0.5 mm; 41 = 0.2 mm.



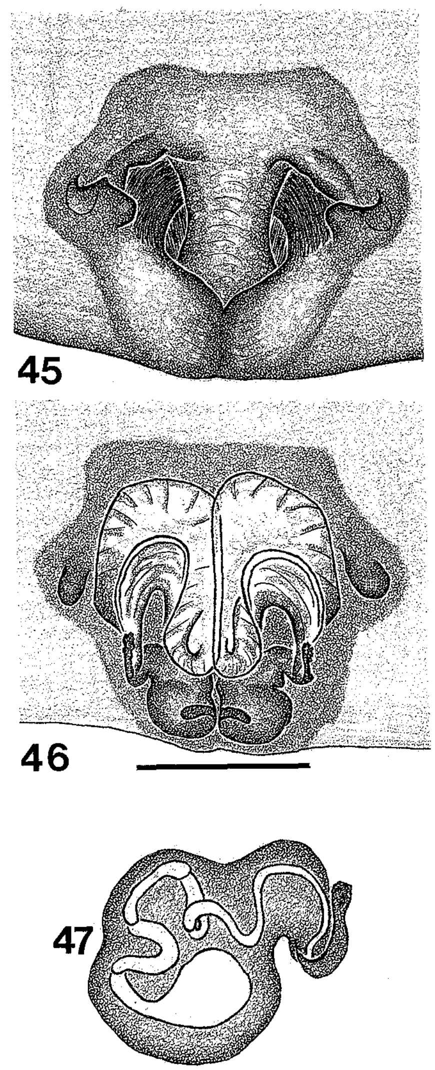
Figures 42–44.—*Perenethis venusta* from Australia (lectotype, ZMUH). 42, Epigynum; 43, Vulva; 44, Left spermatheca, dorsal view. Scale line: 42, 43 = 0.5 mm; 44 = 0.2 mm.

8.53 long, prosoma 3.41 long, 2.83 wide; legs all broken off. Epigynum: As in *P. sindica* (Figs. 36, 39). Vulva: As in *P. venusta* (Figs. 43, 46), spermathecal duct less convoluted than in *P. venusta*. *Male:* Coloration as in female, legs ventrally not dark-gray as in *P. venusta* but yellowish-brown. Measurements: Body 8.33 long, prosoma 3.32 long, 2.6 wide. Leg length: Fe 5.34, PaTi 6.41, MeTa 8.34, total length 20.08. Leg formula: (I, II) IV, III, leg length differences small. Male palp very similar to *P. venusta* (Figs. 57), tibial apophysis short, distal tegular apophysis with wing.

Remarks.—*Perenethis fascigera* may be conspecific with *P. venusta.*

Distribution.—Known from Japan and China.

Specimens examined.—**JAPAN**: *Kyushu*, Ushibuka, ;1♂1♀, 29 July 1978 (Y. Chikuni). Loan: Courtesy of T. Yaginuma.



Figures 45–47.—*Perenethis venusta* from Australia (paralectotype; MCSN). 45, Epigynum; 46, Vulva; 47, Left spermatheca, dorsal view. Scale line: 45, 46 = 0.5 mm; 47 = 0.2 mm.

Perenethis simoni (Lessert 1916)
Figs. 31–33, 51, 52, 54–56)

? *Tetragonophthalma phylla*, –Simon 1898: 293, CONGO: Landana MNHN ES no. 3080; *non vidi* (listed by Blandin 1975a: 379).

Tetragonophthalma simoni Lessert 1916: 577; 2♂,1♀ syntypes; type locality: ♀ lectotype [here designated], KENYA: Nanyuki [specimen label: Ngare na nyuki], Expedition Sjöstedt; NHRS; ♂ paralectotype [right palp missing], juvenile ♂ paralectotype, TANZANIA: Arusha, Kibonoto [presumably Kibongoto], Expedition Sjöstedt; NHRS; *vidi.*

Maypacius berlandi Roewer 1955: 160, *nomen novum*; ♂♀ syntypes; type locality: ETHIOPIA: Barko; MNHN (det. by Berland as *Tetragonophthalma stuhlmanni*); *non vidi*. Synonymy by Blandin 1975a: 379.

Perenethis straeleni Roewer 1955: 265, ♂ holotype, type locality: ZAIRE, Upemba National Park, Mabwe, Lac Upemba; MRAC 119709; *non vidi.* Synonymy by Blandin 1975a.

Perenethis simoni, –Blandin 1975a: 379; 3♂3♀; IVORY COAST, Lamto, MNHN; *vidi.*

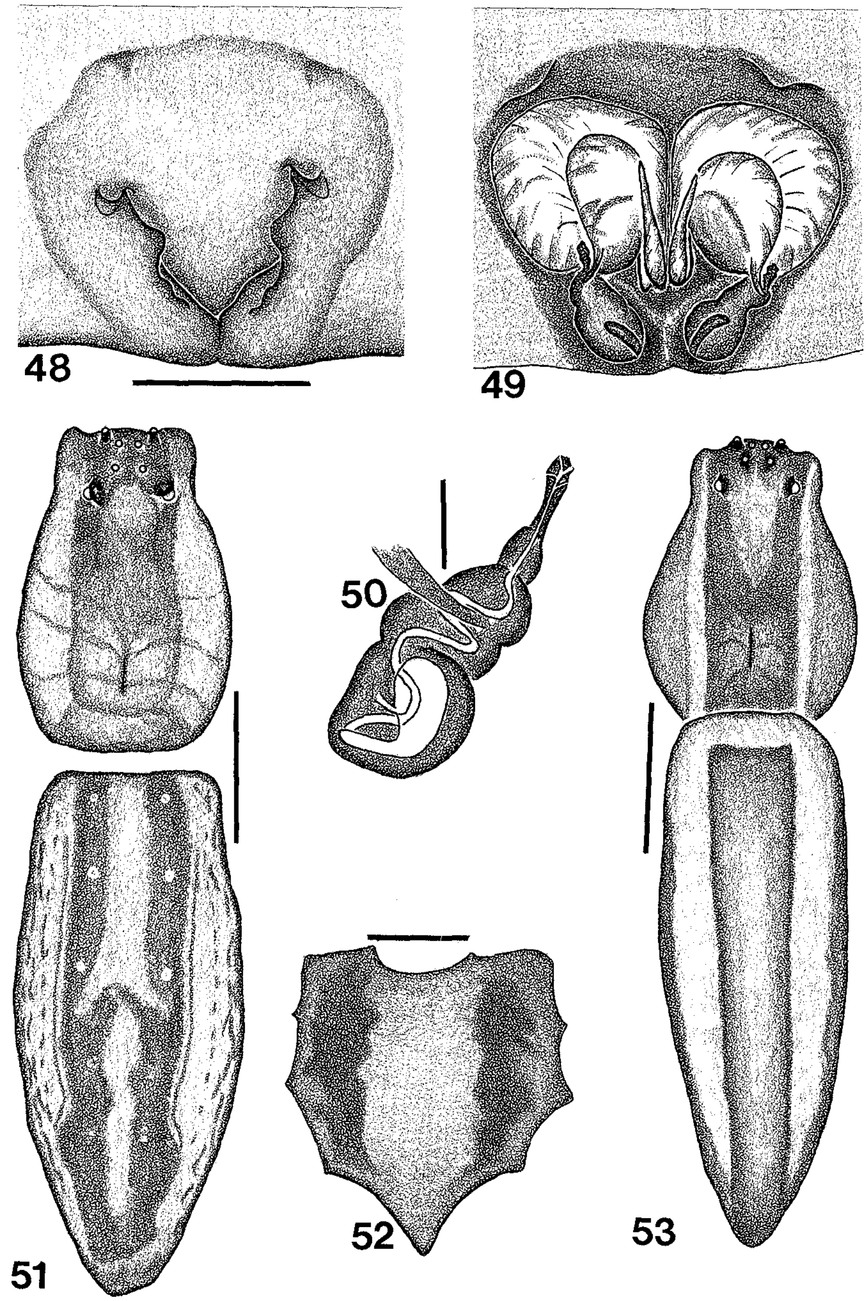
Pisaurellus badicus, –Blandin 1976b: 926, figs. 2, 7b, 8 [non *Pisaurellus badicus* Roewer 1961, see *Perenethis symmetrica* below].

Catalogs: Roewer 1954, 2a: 118. Bonnet 1955, 2: 4361, *sub Tetragonophthalma.* Platnick 1993: 520.

Note: In the original description, Lessert (1916: 580) mentioned three specimens (collected in Kibonoto [2♂, not indicated as subadult] and Ngare na nyuki [1♀] during the Sjöstedt Expedition [1905–1906]). One adult male, one subadult male (labelled Kibonoto) and one female (labelled Ngare na nyuki) are deposited in the Naturhistoriska Rijksmuseet in Stockholm. Female here designated as lectotype. A left male palp (from Kibonoto, MNHNG), labelled syntype, is not part of the adult male syntype from Stockholm (palp is too large). Blandin (1975a: 379) erroneously cited a female in MNHNG as holotype of *T. simoni* [specimen label states: ZAIRE: Garamba]. This female from Zaire, Garamba, was collected during the American Museum Congo-Expedition in 1937.

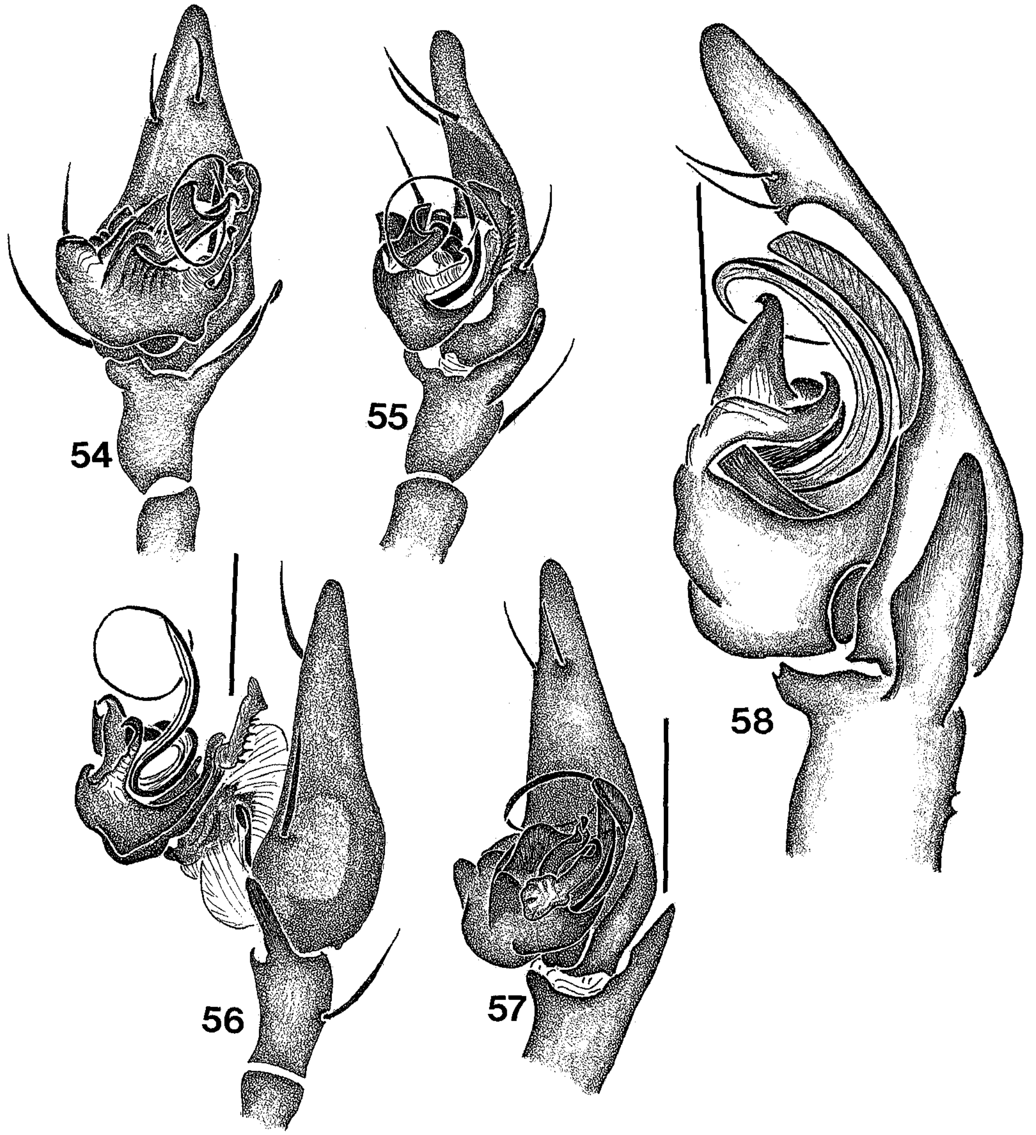
Diagnosis.—Epigynum with straight carina (*ch* 9); head of spermatheca bent dorsally pointing anteriorly (*ch* 16), first loop of spermathecal duct forming a complete circle; male conductor with fringed edge. *P. simoni* very similar to *P. sindica* and *P. venusta*, the latter two with fewer loops in the spermathecal duct. Coloration, structure of male and female copulatory organs similar to *P. venusta* and *P. sindica*.

Description.—*Female:* (7♀). General coloration of body, legs and palps yellowish-brown, prosoma with whitish lateral bands (Fig. 51); opisthosoma with light median band and two whitish stripes laterally; sternum with two dark lateral patches (Fig. 52). Legs ventrally grayish-black, especially the femora. Measurements (♀ lectotype): Body 10.9 long, prosoma 4.0 long, 3 wide. Largest female measured: Body 16 long,



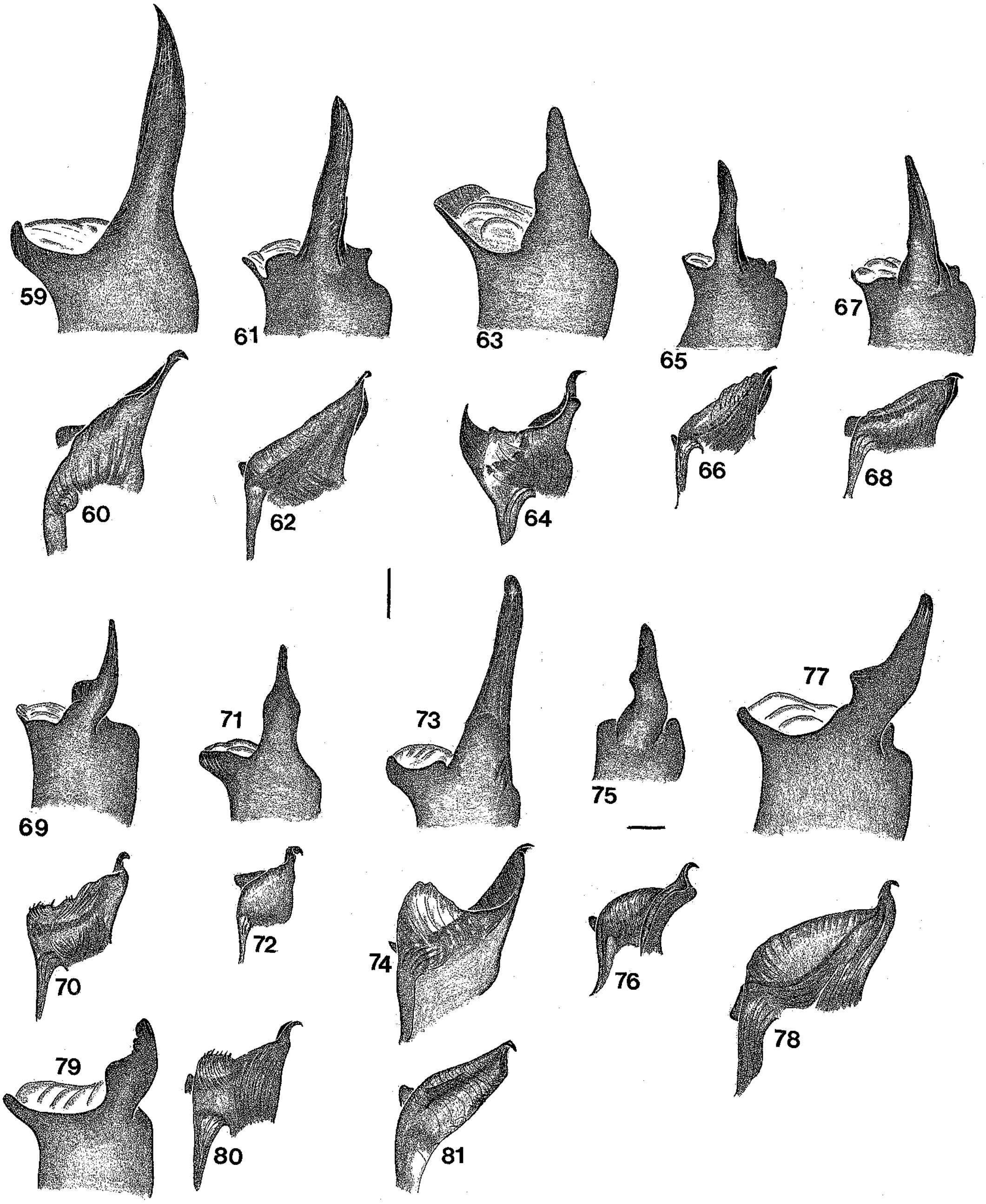
Figures 48–53.—*Perenethis*, female organs and color pattern. 48–50, *P. dentifasciata* from Pakistan or India? (Yarkand Mission, holotype; OXUM). 48, Epigynum; 49, Vulva, 50, Left spermatheca, dorsal view. 51–52.—*P. simoni* from Kenya (lectotype; NHRS): 51, Color pattern sternum; 52, Dorsal color pattern, female. 53, *P. venusta* from Australia, dorsal color pattern (female lectotype; ZMUH). Scale lines: 48, 49 = 0.5 mm; 50 = 0.1 mm; 51 = 1 mm; 52, 53 = 2 mm.

prosoma 4.4 long, 3.3 wide. Leg length (prosoma 4.0 long): Fe 6.4, PaTi 7.8, MeTa 9.166, total length 23.4. Epigynum (Fig. 31): Straight ridge-like carina conspicuous. Vulva (Fig. 32): Copulatory duct saccate and membranous, forming two large loops, first loop slightly wider than second; head of spermatheca ball-shaped (Fig. 33), bent



Figures 54–58.—Left male palp of *Perenethis*. 54–56, *P. simoni* from Ivory Coast (MNHN). 54, Unexpanded, ventral view; 55, Unexpanded, retrolateral view; 56, Expanded, retrolateral view. 57, *P. venusta* from Australia (MCSN), unexpanded, retrolateral view. 58, *P. symmetrica* from South Africa (AMNH), unexpanded, retrolateral view. Scale lines: 54–57 = 1 mm; 58 = 0.5 mm.

dorsally; stalk of spermathecae large and strongly sclerotized; spermathecal duct with five loops, the first loop describing a complete, small circle, the fourth loop tilted dorsally; base of spermatheca with small lumen. *Male:* (5♂). Coloration and pattern as in females. Measurements: Adult paralectotype: Body 15.16 long, prosoma 5.1 long, 3.75 wide. Smallest specimen: Body 11.2 long, prosoma 4.4 long, 3.5 wide. Leg length (prosoma 4.1 long): Fe 7.0, PaTi 9.08, MeTa 11.6, total length 27.7. Male palp (Figs. 54–56): Retrolateral tibial apophysis long and flat (spatula-shaped), tip rounded; short hump-shaped ventral tibial apophysis, forming a projection of the apical tibial edge; median apophysis narrow, with terminal, sclerotized hook; distal tegular apophysis with terminal hook and conspicuous "wing"; conductor narrow, partly ex-



Figures 59–81.—Retrolateral tibial apophysis (odd numbers) and distal tegular apophysis (even numbers) of left male palp. 59–74, *Perenethis sindica*. 59, 60, From India: Bombay (OXUM bottle 1522); 61, 62, From India: Bombay (OXUM bottle 1525); 63, 64, From India: Kanchrapara (AMNH); 65, 66, From Sri Lanka (OXUM bottle 1526, tube A); 67, 68, From Sri Lanka (OXUM bottle 1526, tube B); 69, 70, From Nepal: Bagmati Dist., Kathmandu-Valley, Balaju Park, September 1969 (CM); 71, 72, From East Pakistan or northwest India (Yarkand Mission; OXUM). 73, 74, *P. simoni* from Ivory Coast (MNHN). 75, 76, *P. venusta* from Australia (note different scale line; MCSN). 77—80, *Perenethis* sp., special forms. 77, 78, From Turkey: Smyrna (OXUM); 79, 80, From Nepal: Dhading Dist, between Kagune and Samari Banjyang, 800–1000 m, 23 July 83, agricultural area (CM). 81, *P. symmetrica* from South Africa (AMNH), distal tegular apophysis. Scale lines = 0.2 mm.

pandable, with fringed edge; embolus long, whiplike with pars pendula following ⅔ of embolus length. Leg formula (♂ ♀): (I-II), IV, III.

Natural history.—Occurs in savanna vegetation (Blandin 1975a: 380).

Distribution.—Africa, south of the Sahara.

Specimens examined.—Types listed above. **TANZANIA**: *Arusha*, Kibonoto, Expedition Sjöstedt, 1♂ (left palp only), MNHNG [labelled syntype]. **ZAIRE**: *Garamba* (det. Lessert), American Museum Congo-Expedition, ♀ labelled holotype by Blandin (MNHNG). **IVORY COAST**: *Lamto*, 3♂; 3♀ (MNHN). **SENEGAL**: *Dakar*, km 15 R. Rufisque, 1♀, August 1980 (W. Settle) (CASC). **BOTSWANA**: *Serowe*, 1♀, *ex* malaise trap, March 1990 (P. Forchhammer) (CASC). **ZIMBABWE**: 33 mi SE of Chirundu, 1170 m elev., 1♂, 8 March 1958 (S. Ross & R.E. Leech) (CASC).

Perenethis sindica (Simon 1897)
Fig. 36–41, 59–72

Tetragonophthalma sindica Simon 1897: 295; 2♀ syntypes; type locality: INDIA [near Bombay] Kurrachee (MNHN), *vidi*.

Perenethis indica [sic!], -Pocock 1900: 246; ♀ (BMNH 99.11.2.147), *vidi*.

Catalogs: Roewer 1954, 2a: 118. Bonnet 1955, 2: 4361, *sub Tetragonophthalma*.

Diagnosis.—Female copulatory organ very similar to *P. simoni* and *P. venusta*, spermathecal duct with fewer loops than *P. simoni*. Male retrolateral tibial apophysis often pointed (*ch* 19).

Description.—Chelicerae: Inner tooth at posterior margin twice as large at outer tooth. *Female:* (17♀). Overall coloration yellowish-brown to medium brown; prosoma and opisthosoma dorsally with broad, dark, median band; set off by narrow, straight stripes of silver or white; sternum and opisthosoma ventrally with pale median band. Opisthosoma slender and elongated. Legs uniformly brown. Measurements: Range: Body 8.7 long, prosoma 3.3 long, 2.8 wide (Sri Lanka) to body 20.4 long, prosoma 5.8 long, 4.5 wide (INDIA: West Bengal). Leg length (prosoma 3.75 long): Fe 5.7, PaTi 7.1, MeTa 8.6, total length 21.5. Epigynum (Figs. 36, 39): Very similar to *P. simoni* and *P. venusta*, carina variable. Vulva (Figs. 37, 38, 40, 41): Copulatory duct and spermatheca very similar to *P. simoni* and *P. venusta*; spermathecal duct with four loops; head of spermatheca bent as in *P. simoni* and *P. venusta*; lumen of base of spermatheca large as in *P. venusta* and larger than in *P. simoni*. *Male:* (10♂). Shape, color and color pattern of body and legs as in female. Measurements: Range: Body 8.75 long, prosoma 3.5 long, 2.9 wide (Sri Lanka) to body 16.4 long, prosoma 5.6 long, 4.1 wide (INDIA: Bengal). Leg length (prosoma 3.75 long): Fe 7.08, PaTi 9.16, MeTa 11.1, total length 27.4. Male palp (Figs. 59–72): Palp and genital bulb similar to *P. simoni* and *P. venusta*; distinct ventral tibial apophysis with two-pronged tip, larger than in *P. simoni*; retrolateral tibial apophysis flat and spatula-shaped as in *P. simoni*, but with variations in length and shape, tip pointed. Great variation in distal tegular apophyses, especially in form of hook and wing.

Remarks.—The size range for the specimens appears to be very high. In addition, features of the male copulatory organ are surprisingly variable, but disjunct concordant features can not be found in the sample available for this study (Material from the National Collection in Calcutta was not available for study, Biswas *in litt.* 1987).

Natural history.—No data are available.

Distribution.—India, Sri Lanka, Philippines.

Specimens examined.—**INDIA**: *SE West Bengal*, Kanchrapara, 1♂2♀, July 1944 (AMNH); same locality, 1♂ (AMNH); *Maharashtra*, Bombay, 1♂, (OXUM 1525); same locality, 1♂, (OXUM 1522, tube 90); *Maharashtra*, Pune, 1♀ (BMNH 1899.11.2.147). **SRI LANKA**: 4♂6♀ (OXUM 1526); 1♀ (ZMHB 29225). **NEPAL**: *Dhang Dist. W Samari*, Banjyang/Topal Khola (river), agricultural area, 1000–1200 m, 1♀, 23 July 83 (Martens & Schawaller leg.) (CM 211); *Mechi District*, Taplejung, Kabeli Khola (river), 900–1250 m, agricultural area, forest remains, 1♀, 1 September 83 (Martens & Daams leg.) (CM 267); *Bagmati Dist.*, Kathmandu-Valley, Balaju Park, 1♂1♀, September 69 (CM without number). **PHILIPPINES**: *Luzon*, 1♀ (ZMHB 3847). Locality unknown, "Yarkand-Mission", 1♂1♀ (OXUM).

Perenethis symmetrica (Lawrence 1927)
Figs. 34, 35, 58, 81

Tetragonophthalma symmetrica Lawrence 1927: 46; female holotype; type locality: NAMIBIA: Ongandjera; SAM B 6228; *vidi*.

Perenethis symmetrica, -Roewer 1955: 267.

Pisaurellus badicus Roewer 1961: 40, fig. 5; ♀ holotype; type locality: SENEGAL: Parc National du Niololo-Koba; *non vidi*. Holotype not available from IFAN. NEW SYNONYMY.

Perenethis huberti Blandin 1975a: 382; ♀ holotype, 4♀ and 2 juv. paratypes, type locality: AFAR: Djibouti, MNHN No. 19149; *vidi*. Synonymy by Sierwald 1989a.

Perenethis lejeunei Blandin 1975a: 382; ♀ holotype, ♂ (= paratype); type locality: ZAIRE: Kivu; MRAC 144355; *non vidi*. Synonymy by Sierwald 1989a.

Catalogs: Roewer 1954, 2a: 118. Bonnet 1955, 2: 4361, *sub Tetragonophthalma*. Brignoli 1983: 463, *P. huberti*; page 464, *P. lejeunei*. Platnick 1993: 520.

Taxonomic note: The specimen figured by Blandin (1976b: fig. 8, male palp) as *Pisaurellus badicus* is not conspecific with *P. badicus* Roewer 1961, but belongs to *Perenethis simoni*. Roewer's figures (1961: fig. 5 c,e,d) of the palp establish the synonymy of *Pisaurellus badicus* with *Perenethis symmetrica*.

Diagnosis.—Color pattern distinctive (Blandin 1975a: figs. 8, 10): Opisthosoma dorsally with dark, lobed median band; carina of epigynum curved like eyebrows (*ch* 9); both loops of membranous copulatory duct of approximately same size (*ch* 15); embolus distinctive, broad pars pendula reaching tip of embolus (*ch* 34); smallest species of the genus.

Description.—Chelicerae: Inner tooth at posterior margin only slightly larger than outer tooth. Leg formula: (I-II), IV, III. Very little variation in color pattern and copulatory organs. *Female:* (11♀). Prosoma: Dorsally with dark median band, thin bright line in the middle, and laterally two broad light-yellow longitudinal bands; sternum yellow with three dark-gray spots at each side; opisthosoma dorsally with dark, lobed median band (straight in all other species of *Perenethis*); sides yellowish with irregular brown markings; venter yellowish without pattern. Legs: Femora to tibia of first three legs ventrally dark gray. Palps with black rings at joints. Measurements: Type *P. symmetrica*: Body 8.5 long, prosoma 2.5 long, 2.0 wide. Range: Body 5.7 long, prosoma 2.1 long, 1.8 wide to body 8.5 long, prosoma 2.5 long, 2.0 wide. Leg length (prosoma 2.3 long): Fe 3.1, PaTi 3.8, MeTa 4.0, total length 11.0. Epigynum (Fig. 34): Carina curved, forming "eyebrows." Vulva (Fig. 35): Copulatory duct membranous, in two large, nearly equal-sized loops; spermatheca large, head of spermatheca round, pointing laterally; stalk thick, spermathecal duct with seven loops; base of spermatheca with small lumen. *Male:* (15♂). Shape, color and color pattern of body and legs similar to female. Legs ventrally lighter gray, only light markings at palps. Measurements: Body 5.3 long, prosoma 2.3 long, 1.7 wide to body 7.2 long, prosoma 3.0 long, 2.7 wide. Leg length (prosoma 2.3 long): Fe 4.2, PaTi 5.3, MeTa 6.2, total length 15.7. Male palp (Figs. 58, 81): Ventral tibial apophysis distinct with swollen tip; retrolateral tibial apophysis spatula-shaped, with rounded tip, little variation in the examined sample; conductor slender, edge without fringe; median apophysis with rather large, sclerotized hook; distal tegular apophysis with small hook, without wing; embolus moderately long, pars pendula nearly reaching tip of embolus.

Natural history.—Occurs in shrubs (Blandin 1975a).

Distribution.—Africa, south of the Sahara, reaching well into South Africa.

Specimens examined.—Types listed above. **SOUTH AFRICA**: *Transvaal*, Kruger Park, Skukuza, in thornscrub, 12♂, 15 December 1985 (AMNH); *east Transvaal*, 15 km from Klaserie, Guernsey Farm, woodland, 5♂4♀4juv♀, 19–31 December 1985 (AMNH). **TANZANIA**: *Tabora*, 1♂ (ZMHB 29226). **KENYA**: *Lake Nakuru National Preserve*, campsite in yellow fever forest, 5♂4♀, 14 May 1975 (A.J. Penniman leg.) (AMNH). **ZAIRE**: *Epulu*, 250 m, 1♂, 2 October 57 (E.S. Ross & R.E. Leech) (CASC).

Perenethis venusta L. Koch 1878
Figs. 42–47, 53, 57, 75, 76

Perenethis venusta L. Koch 1878: 980; 3♀ syntypes; type locality: AUSTRALIA, Queensland. ♀ lectotype here designated; ZMUH, *vidi*. ♀ paralectotype: Rockhampton; ZMHB 3501 (opisthosoma missing); *vidi*. ♀ paralectotype: Peak Down; BMNH; *vidi*.

Perenethis venusta, –Thorell 1881: 372; ♂♀ specimens, locality: AUSTRALIA: Queensland, Cape York Peninsula; MCSN; *vidi*.

Perenethis unifasciata, –Thorell 1891: 61; *P. venusta* placed in synonymy of *P. unifasciata*.

Perenethis parkinsoni Dahl 1908: 228; ♀ holotype, type locality: PAPUA-NEW GUINEA: Bismark-Archipelago, Ralum; ZMHB 29 224; *vidi*. Specimen demounted from microscope slide. NEW SYNONYMY.

Perenethis unifasciata, –Chrysanthus 1967: 421; several ♂♀ specimens from INDONESIA: New

Guinea, Merauke and Mindiptana; *non vidi*, figures agree with *P. venusta*.

P. venusta, –Chrysanthus 1967: 421, fig. 58, figure probably based on a subadult *Perenethis* female; removed *P. venusta* from synonymy of *P. unifasciata*.

Perenethis venusta, –Todd-Davies 1985: 104.

Catalogs: Roewer 1954, 2a: 118, as synonym of *P. unifasciata*. Bonnet 1955, 2: 4361, *sub Tetragonophthalma*, as synonym of *P. unifasciata*. Platnick 1993: 520.

Taxonomic note.—*P. parkinsoni* is based on a single female specimen. The female copulatory organ is very similar to Thorell's *venusta* specimen; (Figs. 45–47).

Diagnosis.—Color pattern and copulatory organs very similar to *P. simoni* and *P. sindica*, spermathecal duct with fewer loops than *P. simoni*.

Description.—Chelicerae: Inner tooth of both teeth at posterior margin distinctly larger than outer tooth. Leg formula: (II-I), IV, III. *Female:* (13♀). Coloration light yellowish-brown. Many specimens with dark-grayish coloration on the ventral side of femora, dark gray spots on the coxae and two dark-gray patches on the sternum as in *P. simoni* (Fig. 51). Dorsal color-pattern (Fig. 53) very consistent, prosoma with dark median band and light lateral zones. Two thin stripes of white hairs separate median zone from lateral zones. Opisthosoma with straight dark median band, two thin stripes of dark hair separating the median band from the light-colored lateral zones. Ventral color-pattern: Light median band caused by guanine, laterally two thin dark bands followed by two white bands formed by hair. Lateral parts of opisthosoma covered with grayish-brown hair. Measurements lectotype (ZMUH): Body 10.4 long, prosoma 3.9 long, 2.9 wide. Females slightly smaller than males, legs shorter. Range [13♀]: Body 7.7 long, prosoma 2.87 long, 2.25 wide; to body *ca.* 13 long, prosoma 4.5 long, 3.2 wide. Leg length (prosoma 4.14 long): Fe 5.96, PaTi 7.63, MeTa 8.36, total length 21.95. Epigynum in two rather distinct forms (Figs. 42, 45) both equally common. Carina branches either nearly adjoining in the middle or distinctly separated; external copulatory opening rather large. Vulva (Figs. 43, 44, 46, 47): Copulatory duct membranous, wide and saccate, forming two loops, second loop much narrower than first. Small head of spermatheca and adjacent slender stalk of spermatheca bent dorsally; this part of the spermatheca is smaller than in *P. sindica*. Remaining spermatheca thick and heavily sclerotized; spermathecal duct either with three or four loops, loops slightly variable; size of lumen of base of spermatheca rather large but variable. Variable features of vulva not correlated with either epigynum-type. Female copulatory organ very similar to *P. sindica* and *P. simoni*. *Male:* (7♂). Coloration and color pattern as in females, somewhat lighter. Measurements [7♂]: Males slightly larger than females with longer legs; body 10.6 long, prosoma 4.0 long, 2.8 wide to body 12.0 long, prosoma 4.72 long, 3.56 wide. Leg length (prosoma 4.07 long): Fe 6.98, PaTi 9.16, MeTa 10.61, total length 26.76. Male palp (Figs. 57, 75, 76): Very similar to *P. simoni* and *P. sindica*; retrolateral tibial apophysis (Fig. 57) long and flat (spatula-shaped), tip bluntly pointed; tibial apical margin with low projection similar to *P. simoni*; median apophysis narrow, with terminal, sclerotized hook, membranous base of median apophysis enlarged; distal tegular apophysis with terminal hook and conspicuous "wing" (Fig. 76); conductor genus-typical, slender, without fringe; embolus long, whip-like with conspicuous pars pendula. Form of retrolateral tibial apophysis, median apophysis and distal tegular apophysis show very little variation within the Australian specimens; the male from Singapore very similar as well.

Natural history.—Occurs in grassland and forests (specimen labels; QMBA); Koh (1989).

Distribution.—Thailand, Singapore, Australia and Papua New Guinea.

Specimens examined.—AUSTRALIA: *Queensland*: Homeval, northeast Qld, 1♀ (QMBA S14 644). Eureka Ck, 1♀, 2 February 72 (QMBA S 14 634). Rundle Ra, northeast QLD, 1♀, 31 March 75 (QMBA S14 648). Doboy Ck, southeast QLD, 1♂1♀, 9 January 79 (QMBA S14 632). Brisbane, 1♀ with egg sac, 16 March 86 (QMBA S14 630). Bald Hills, southeast QLD, 1♀, 20 December 79 (QMBA S14 636). Bald Hills, 1♂, 10 January 80 (QMBA S14 639). Cape Hillsborough, N.P. grass area, 1♀, 5 January 75 (QMBA S14 643). Bundaberg forest, southeast QLD, 1♀ (QMBA S14 629). Newroy Is. N.P., 1♂, 14 February 75 (QMBA S14 638). Currumbin, southeast QLD, 1♂, 11 January 80 (QMBA S14 633). Weipa, 1♂, 7 February 75 (QMBA S14 641). 12 samples with juveniles from

Queensland Museum. **SINGAPORE**: Mac Ritchi Reservoir, in grass, 1♀ (Koh 89.07.13.08). Malcolm Road, grassy waste land, 1♂, (Koh 85.08.24.01). **PAPUA NEW GUINEA**: *Madang Province*, Sapi Forest Reserve, 30 km west of Madang, 5°12′S, 145°30′E, 1♀, 4 July 1988 (W.J. Pulawski) (CASC). Vogelkop, Manokwan, 75 m, 1♀, 21 July 1951 (D. Elmo Hardy) (BPBM). Waris, 450 m, 1♀, VII-VIII (T.C. Maa) (BPBM). **THAILAND**: 8 mi SE Saraburi, 100 m, 1♂, 28 July 62 (E.S. Ross & D.Q. Cavagnaro) (CASC).

Special forms.—The material examined for this study contained two males that cannot be placed in any described *Perenethis* species. Due to the uncertainty of species discrimination between *P. fascigera*, *P. simoni*, *P. sindica* and *P. venusta* on one hand, and the unusual variability in *P. sindica* on the other hand, descriptions of new species-group taxa do not appear justified at this point.

Form I (Figs. 77, 78): Male from Turkey: Smyrna, OXUM. The specimen is similar to *P. simoni*, but the retrolateral tibial apophysis possesses an anterior basal projection. Form II (Figs. 79, 80): Male from Nepal [Dhading Dist, between Kagune and Samari Banjyang, 800–1000 m, 23 July 83, agricultural area, CM]. In this specimen the shape of the retrolateral apophysis is different and does not fit the overall pattern found in *P. sindica*. Since the shape of the retrolateral tibial apophysis is often species-typical in Pisauridae, this specimen could belong to a species distinct from *P. sindica*; it may represent the male of *P. dentifasciata*.

NOMINA DUBIA

Perenethis brevipes (Strand 1906)

Tetragonophthalma brevipes Strand 1906: 685; holotype juvenile (lost), type locality: Sudan, Harerge Mountains; Naturkunde-Museum Stuttgart.

Perenethis brevipes, –Roewer 1955: 267. *P. brevipes*, –Blandin 1975a: 384; *nomen dubium*

Ctenus marginatus Walckenaer 1847

Ctenus marginatus Walckenaer 1847: 402, ♀ ?holotype; type locality: Solomon Islands; type presumed lost.

Thalassius marginatus, –Simon 1891: 299.

Walckenaer compares the specimen to *Pisaura mirabilis*. This could suggest that Walckenaer's specimen was congeneric with *Perenethis* (general color pattern and habitus). Simon's (1891) placement of this species in the genus *Thalassius* was rejected (Sierwald 1987).

Perenethis rectifasciata (O. Pickard-Cambridge 1885)

Ocyale rectifasciata O. Pickard-Cambridge 1885: 78; juvenile male holotype; type locality: northeast PAKISTAN or north-west INDIA ("Murree to Sind valley and Sind valley"); OXUM; *vidi*.

Pisaura rectifasciata, –Simon 1898a: 289.

Catalogs: Roewer 1954, 2a: 121, *sub Pisaura*. Bonnet 1955, 2: 3681, *sub Pisaura*.

Based on eye-pattern and number of teeth at the chelicerae, the subadult male is a member of the genus *Perenethis*. Color-pattern faded, most spines lost. *P. rectifasciata* is here considered a *nomen dubium*.

Perenethis unifasciata (Doleschall 1859)

Dolomedes unifasciata Doleschall 1859: 10; ♀ holotype lost; type locality: Indonesia: Amboina.

Perenethis unifasciata, –Thorell 1891: 61.

Tetragonophthalma unifasciata, –Strand 1911: 165, ♀ from INDONESIA: Kepulauan Aru Islands, Pulau Kobroor. Specimen not in SMFD (*fide* Chrysanthus 1967).

Catalogs: Roewer 1954, 2a: 118. Bonnet 1955, 2: 4361, *sub Tetragonophthalma*.

According to the collection catalog in the Museum for Natuurlijke Historie in Leiden the female specimen figured in Doleschall's publication (1859, fig. 6) never arrived in Leiden (van der Hammen pers. comm. 1982). Therefore, no actual type-specimen exists. The specimen figured could be conspecific with *venusta*. *P. unifasciata* is here considered a *nomen dubium*.

Maypacius Simon 1898

Figs. 82–87, 91–96

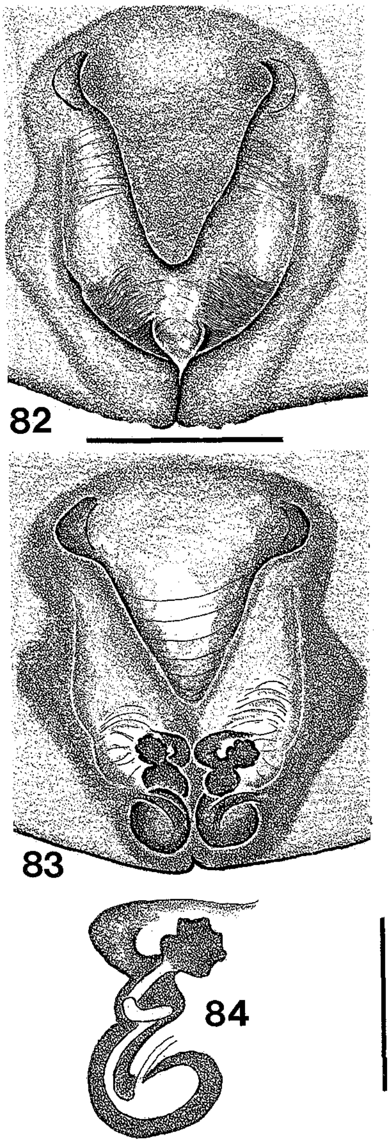
Maypacius Simon 1898a: 292. Type species, by original designation, *Maypacius vittiger* Simon 1898b: 13; female holotype, Madagascar & Africa.

Blandin (1975a, 1978b) recognized nine species in the genus *Maypacius* and listed a total of 21 specimens, only six of them males; five species are known from females only, two from males; for two species both sexes are recognized. Species: *Tetragonophthalma bilineatus* Pavesi 1895, ♀ known; *Maypacius christophei* Blandin 1975 (1975a), ♀ known; *Maypacius curiosus* Blandin 1975 (1975a), ♂ known; *Maypacius gilloni* Blandin 1978 (1978b), ♂♀ known; *Maypacius kaestneri*

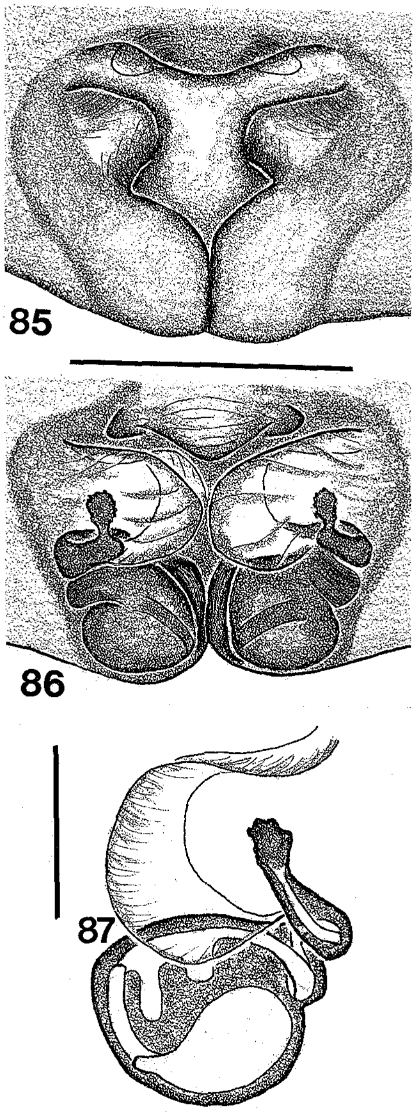
Roewer 1955, ♂♀ known; *Maypacius petrunkevitchi* Lessert 1933, ♀ known; *Maypacius roeweri* Blandin 1975 (1975a), ♂ known; *Maypacius stuhlmanni* Bösenberg & Lenz 1894, ♀ known; *Maypacius vittiger* Simon 1898 [Simon 1898b: 13], ♀ known. *Maypacius vittiger* was synonymized with *Tetragonophthalma bilineatus* Pavesi 1895 by Simon (1906: 1169); Roewer (1955: 153) listed *M. vittiger* as junior synonym of *Maypacius bilineatus*; Blandin (1974a: 309; 1975a: 385) removed *M. vittiger* from the synonymy of *M. bilineatus*.

Diagnosis.—Two equally-sized cheliceral teeth (*ch* 0, 1), short copulatory duct (*ch* 15), short spines (*ch* 6), and the following autapomorphic characters: Strongly procurved AER (*ch* 2), ALE on tubercles and located nearly beneath AME; conductor short (*ch* 23), with specialized apical region with two guiding lamellae (*ch* 28). Synapomorphic characters: Two cheliceral teeth at retromargin (*ch* 0) and retrolateral peak at tegulum (*ch* 21) shared with *Polyboea* and *Perenethis*; conductor with two guiding lamella (*ch* 28), pit in dorsal branch of distal tegular apophysis (*ch* 29) and shape of sclerite *A* shared with *Polyboea* (*ch* 31).

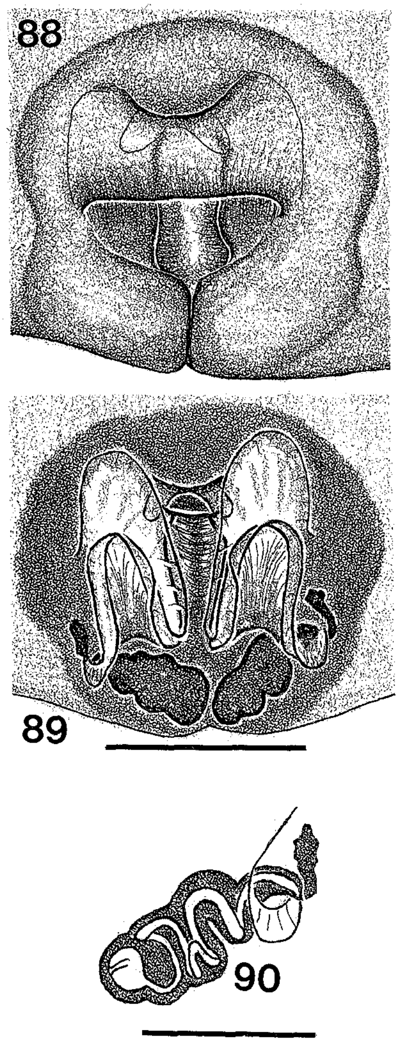
Description.—Based on *M. kaestneri*, *M. petrunkevitchi*, and *M. roeweri*. Measurements: *M. kaestneri*: ♀: Body 12.43 long, prosoma 3.56 long, 2.6 wide (MRAC 142.407). Leg length: Fe 6.6, PaTi 7.8, MeTa 8.7, total length 23.2. *M. petrunkevitchi*: ♀: Body 13.45 long, prosoma 2.9 long, 2.18 wide. Leg length: Fe 5.45, PaTi 6.6, MeTa 7.2, total length 19.25 (MRAC 145.395). *M. roeweri*: ♂: Body 11.81 long, prosoma 3.45 long, 2.7 wide. All legs broken off. Eye pattern: AE in two rows (AER extremely procurved); ALE on tubercles, in front of AME and only slightly further apart from each other than AME; PLE=AME>PME=ALE. Eyes small compared to body size, PME:AME = 0.7–0.8; AME:ALE = 1.5. Chelicerae: Posterior margin with two equally-sized teeth, teeth closer to outer edge of chelicerae and wider spaced than in *Perenethis*. Spine pattern identical with *Charminus camerunensis*. Spine length: Spines very short; spine length:tibia width = 1. Epigynum (*M. petrunkevitchi* and *M. kaestneri*, Figs. 82, 85): Continuous carina weakly developed, anterior edge conspicuous, carina straight or recurved (strongly recurved in *M. petrunkevitchi*); fossae mesal to copulatory opening. Vulva (Figs. 83, 84, 86, 87): Membranous copulatory duct short, forming single curve; *M. petrunkevitchi*: Copulatory duct sclerotized close to the spermathecae, head of spermatheca pointing anteriorly, spermathecal duct forming single loop, base of spermatheca with small lumen; *M. kaestneri*: Head of spermatheca bent, spermathecal duct with two loops, base of spermatheca with large lumen.



Figures 82–84.—*Maypacius petrunkevitchi* from Rwanda (MRAC 145.395). 82, Epigynum; 83, Vulva; 84, Left spermatheca, dorsal view. Scale lines: 82, 83 = 0.5 mm; 84 = 0.2 mm.



Figures 85–87.—*Maypacius kaestneri* from Ghana (MRAC 142.407). 85, Epigynum; 86, Vulva; 87, Left spermatheca, dorsal view. Scale lines: 85, 86 = 0.5 mm; 87 = 0.2 mm.



Figures 88–90.—*Polyboea vulpina* from Singapore (NMSC). 88, Epigynum; 89, Vulva; 90, Left spermatheca, dorsal view. Scale lines: 88, 89 = 0.5 mm; 90 = 0.2 mm.

Male palp (based on *M. roeweri*, Figs. 91–96): Retrolateral tibial apophysis pointed, directed forward (perpendicular in *M. curiosus*); tegulum with conspicuous, retrolateral peak; short conductor with narrow base and uniquely enlarged tip, embolus resting between two lamellae; distal tegular apophysis with hook and wing, dorsal branch of distal tegular apophysis with pit as in *Polyboea*; sclerite *A* large, forked, similar to *Polyboea*; distal sclerotized tube similar to *Polyboea*; embolus short, with wide pars pendula, about ½ embolus length. For the cladistic analysis, characters for the male of *M. kaestneri* were taken from Blandin's figure (1975a: 389, fig. 21, 22).

Natural history/habitat.—Occurs in the savanna, found in vegetation (Blandin 1978b).

Specimens examined.—*M. roeweri:* **ZAIRE**: *Kivu*, Uvira, Mugesera, 1♂ paratype (MRAC 145.058). *M. petrunkevitchi:* **RWANDA**: *Burgesera*, Biharagu, found in dense field vegetation, 1♀ (MRAC 145.395); Butare, 2♀ (MRAC 140.720). *M. kaestneri:* **GHANA**: *Legon*, 1♀ (MRAC

142.407). **CONGO**: *Faradje*, 1♀ (MRAC 145.400).

Polyboea Thorell 1895
Figs. 88, 90, 97–101

Polyboea Thorell 1895: 228. Type species, by original designation, *Polyboea vulpina* Thorell 1895: 229, juvenile male holotype, Burma: Rangoon).

The genus is based on a subadult male of the type species from Burma. Male and female copulatory organs from specimens collected in Singapore are figured here for the first time. Currently, the genus is monotypic. The Asian pisaurid genus *Eurychoera* Thorell 1897 (listed in the Pisaurinae by Roewer, 1955: 115) from Singapore (Koh 1989: 97) is not closely related to *Polyboea.*

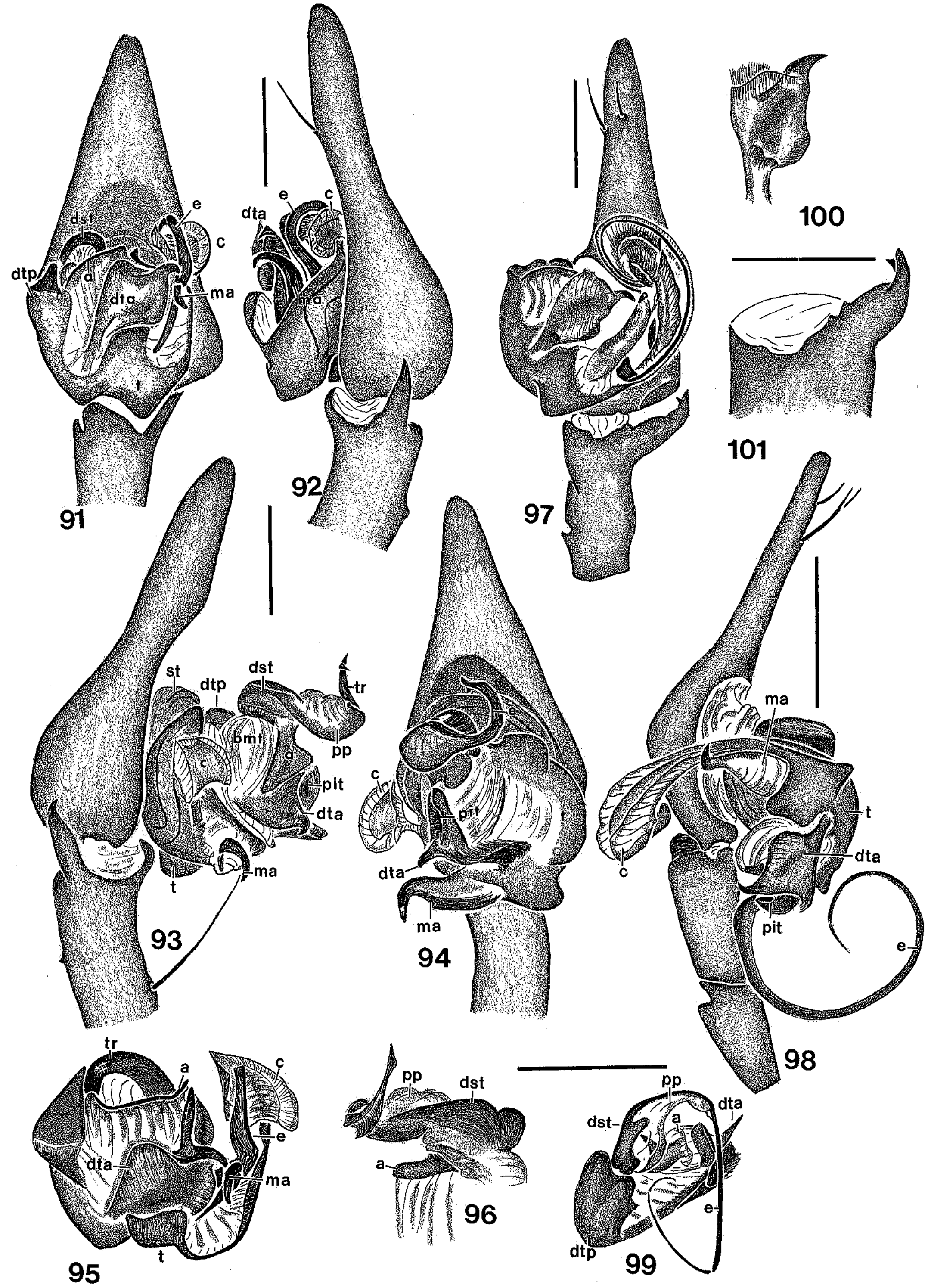
Diagnosis.—AER procurved (*ch* 2), two equally-sized cheliceral teeth (*ch* 0) and the following autapomorphic characters: ALE significantly larger than PME (*ch* 3) and AME (*ch* 4); chelicerae longer than in all other perenethine genera; absence of the two paired short spines apically at the ventral side of the tibia. Since the genus is currently monotypic, characters listed here may be apomorphic at species level. Synapomorphic characters: Two cheliceral teeth at retromargin (*ch* 0) and tegulum with retrolateral peak (*ch* 21) shared with *Perenethis* and *Maypacius*; copulatory duct with two wide membranous loops shared with *Perenethis* and *Charminus camerunensis* (*ch* 14), conductor with two guiding lamellae (*ch* 28), pit in dorsal branch of distal tegular apophysis (*ch* 29) and shape of sclerite *A* shared with *Maypacius* (*ch* 31).

Polyboea vulpina Thorell 1895
Figs. 88–90, 97–101

Polyboea vulpina Thorell 1895: 229.
Polyboea vulpina, –Workman & Workman 1897: 97 (= *Ocyale hirsuta* on plate 97.); *non vidi.*
Polybaea[*sic*] *vulpina*, –Simon 1898a: 289, 296
Polyboea vulpina, –Hasselt 1899: 174
Polyboea vulpina, –Koh 1989: 100 (color photo of ♂)
Catalogs: Petrunkevitch 1928: 102, as *Polybaea.* Roewer 1954, 2a: 122, as *Polybaea.* Bonnet 1955, 2: 3751. Genus listed: Brignoli 1983: 461, *Polybaea*; Platnick 1989: 393, *Polybaea*; Platnick 1993: 521, *Polyboea.*

Diagnosis.—Chelicerae large, spines long, tibia lacks apical ventral spine pair; epigynal folds parallel and apart from each other anteriorly; carina forming lip with straight posterior edge; long conductor with curved tip, similar to conductor in the west African *Maypacius gilloni* (Blandin 1978b: fig. 2).

Description.—Eye pattern: AER procurved; AER nearly as wide as PER, ALE>PLE=PME>AME. AME conspicuously smaller than PME, PME:AME = 1.6; AME:ALE = 0.5. Chelicerae: Posterior margin with two nearly equally-sized teeth, teeth closer to outer edge of chelicerae and wider spaced than in *Perenethis*; chelicerae in both sexes longer than in other Pisauridae, prosoma width:chelicerae-length = 1.7; compare to *Maypacius roeweri* ♂: prosoma width:chelicera length = 2.7; *petrunkevitchi* ♀: 2.39; *kaestneri* ♀: 3.3. Spine pattern (Table 6): Pro- and retrolateral femoral spines variable within a single specimen. The absence of two paired short spines apically at the ventral side of the tibia is unique within the Pisaurinae. Spine length: Spines very long; spine length:tibia width = 6.5. *Female:* (1♀). Light orange-yellow, pattern faded (but see male coloration below). Measurements: Body 6.03 long, prosoma 2.5 long, 2 wide. Epigynum (Fig. 88): Epigynal folds parallel and apart from each other anteriorly; adjoining posteriorly; carina forming lip with straight posterior edge, overhanging copulatory opening; fossae close together, mesal to the copulatory openings. Vulva (Figs. 89, 90): Copulatory duct wide and membranous, forming two saccate loops as in *Perenethis*, first loop larger than second loop; head of spermatheca bent, pointing anteriorly; spermathecal duct with four loops; base of spermatheca with small lumen. *Male:* (7♂). Carapace, legs and sternum light orange-yellow, abdomen dorsally with distinct gray-beige Y-shaped figure, the anterior lateral stripes of the Y meet behind the heart, a pair of distinct white spots lateral to the median tail-stripe of the Y. Abdomen ventrally with two parallel narrow dark lines. Measurements: Body length 9.16–10.6, prosoma 3.08—3.6 long, 2.36–2.96 wide. Leg length (prosoma 3.6 long): Fe 6.3, PaTi 8.16, MeTa 9.4, total length 23.8. Male palp (Figs. 97–101): Retrolateral tibial apophysis perpendicular, tip with two pointed ends; tegulum with conspicuous peak at retrolateral corner; long conductor with narrow base and broad tip; tip curved in a spiral; two long guiding lamellae, especially visible in the expanded palp; distal tegular apophysis small, with fringed wing; sclerite *A*



Figures 91–101.—*Maypacius roeweri* and *Polyboea vulpina*. 91–96, *Maypacius roeweri* from Zaire (MRAC 145.058). 91, Unexpanded left palp, ventral view; 92, Unexpanded left palp, retrolateral view; 93, Expanded right palp, retrolateral view, pit indicates pit in distal tegular apophysis; 94, Expanded right

large with the straight edge visible in the unexpanded palp as in *Maypacius*, forked distal end towards the distal sclerotized tube; embolus moderately long; pars pendula short and wide as in *Maypacius*.

Natural history/habitat.—Hasselt (1899) and Koh (1989) report that *P. vulpina* occurs in grasses and low shrubs, building "large, three-dimensional webs that may be connected with one another." This may indicate some form of colonial habit.

Distribution.—Known from Thailand, Malaysia and Singapore.

Specimens examined.—SINGAPORE: no locality given, 1♀ (NMSC 1990.600). Mac Ritchie Reservoir, grasses, 1♂ (Koh 77.01.01.03). **THAILAND**: *Khao*. Yai Nat. Park, 750 m, 2♂, 26 July 1962 (E.S. Ross & D.Q. Cavagnaro) (CASC). 10 mi N Saraburi, 100 m, 1 juv.♂, 11 July 1962 (E.S. Ross & D.Q. Cavagnaro) (CASC). 20 mi S.E. Chantaburi, 75 m, 2♂, 1 August 1962 (E.S. Ross & D.Q. Cavagnaro) (CASC). **MALAYSIA**: Fraser's Hill, 4200 m, 1♂, 2juv., 17 June 62 (E.S. Ross & D.Q. Cavagnaro) (CASC).

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palp, ventral view; 95, Unexpanded left palp, embolic division, top view; 96, Expanded right palp, embolic division, lateral view. 97–101, Left male palp of *Polyboea vulpina* from Singapore (Coll. Koh)., Singapore. 97, Unexpanded, ventral view; 98, Expanded, prolateral view, pit indicates pit in distal tegular apophysis; 99, Same, embolic division, top view; 100, Apophysis distal tegular apophysis; 101, Retrolateral tibial. Scale lines = 0.5 mm.

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