Spermatophores and Spermatophore Producing Internal Organs of Cleridae (Coleoptera: Clerinae): Their Biological and Phylogenetic Implications

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Abstract

Apomorphies of the internal reproductive organs relevant to production and utilization of spermatophores, biologic traits associated with anthophily, and presence of afferent peg sensilla on the antennae suggests that a presumed monophyletic assemblage of genera of subfamily Clerinae are descendants of an ancient monophyletic stock linked to early angiosperm evolution. The species examined include all suprageneric categories of Cleridae proposed to date. The ground plan of the internal reproductive organs of Cleridae for the male involved a pair of multifollicular testes, tubular vas deferens, unichambered seminal vesicle, one pair of accessory glands, highly muscular ejaculatory duct, and for the ancestral female, a pair of multifollicular ovaries, non capsular spermatheca, well-developed spermathecal gland and spermathecal gland duct, and a spacious vagina. Based on presumed homologies of the male accessory glands across generic lines, and to a lesser extent on extraction of contents of the vagina of gravid females, the following clerines are thought to utilize the "mating plug" type of spermatophore as a method of sperm transference: *Trichodes*, *Aulicus*, *Chilioclerus*, *Opilo*, *Dieropsis*, *Phlogistus*, *Phlogistomorpha*, *Scrobiger*, *Trogodendron*, *Zenithicola*, and *Balcus*. Many species of several of the noted genera are anthophilic; histological work involving the alimentary canal, and examination of midgut contents, confirm their pollen feeding habits, and their opportunistic predatory nature on flower-visiting insects. The abovementioned genera are morphologically diverse externally, but nine share a peculiar microsetose character of the antennal club that is presumed synapomorphic. Investigations involving electron microscopy show that some of these microsetae are peg sensilla, which in other beetles are known to function as thermoreceptors. It is hypothesized that these thermoreceptors present on the antenna of spermatophoral clerines are afferent structures that enable the beetles to avoid fire-death in xeric environments. The widespread distribution, peculiar structure of the internal reproductive organs, substantial diversity of external structure, and anthophilous character invite the speculation that the spermatophoral clerines represent a monophyletic group evolved from an ancient Gondwanan ancestor tied to early Angiosperm diversification. Then, due to tectonic, climatic, and ecological events, the spermatophoral clerines became vicariously distributed onto the North American, Eurasian, African, and Australian plates on which they underwent an extensive radiation in part due to Angiosperm proliferation.

Apomorphies of the reproductive organs relevant to the production and utilization of spematophores, biologic characteristics associated with anthophily, and presence of peg sensilla on the antenna suggest that spermatophoral clerine genera may comprise a monophyletic assemblage linked to ancient angiosperm evolution. The impetus for these ideas originate from a ongoing global study of the internal anatomy of Cleroidea whose main objective is to search for apomorphic characteristics to further elucidate Cleroidea phylogenetics.

Of utmost importance in Hennig's methods of phylogenetic analysis (Hennig 1966) is the stringent requirement that only derived (synapomorphous) character states are used for inferences of kinships and monophyly. The search and success for finding

synaptomorphic character states may be greatly enhanced by expanding our search for such information among structural variations of the internal organs.

A comprehensive morphological analysis of the internal organs of Cleroidea is in progress. During the study, it was discovered that among the Cleridae there are several widely distributed genera of the subfamily Clerinae that implement the spermatophoral method of sperm transference. Further, the structural characteristics of the spermatophoral gland and spermathecal capsule suggest a commonality in evolutionary descent. Many of these spermatophoral species are known to frequent flowers and histological cross-sections of the alimentary canal confirms that they feed on pollen. It is believed that along with the development of spermatophoral method of sperm transference there evolved a trophic function of the spermatophore which serves to nourish the female when food becomes scarce amidst an anthophilic lifestyle.

The purpose of this paper is threefold: 1) to call attention to the extensive structural diversity one may find among the internal reproductive organs of the checkered beetles; 2) to examine some possible phylogenetic relationships among spermatophoral clerine genera, largely on the basis of peculiar configurations of spermatophoral glands and spermathecae; and 3) to urge collection- oriented institutions to establish collections of specimens in a suitable liquid preservative so that students of insect systematics have greater access to character states of the total morphology of their study organisms.

A more detailed, more taxa comprehensive, treatment of Cleridae and Cleroidea internal anatomy is in preparation and will be augmented as additional fluid-preserved specimens become available. Further, the brief comparisons among the included genera and species bring a greater focus on a set of reproductive organ components that seem to express ancient Old World-New World relationships among an assemblage of Clerinae genera. This work is the third of a series of publications whose purpose is to make available information of the internal morphology of Cleridae and Cleroidea (Ekis and Gupta 1971; Ekis 1978). Variations of the internal organs, and in particular those of the reproductive systems, represent a heretofore underutilized inventory of systematic information for studies in beetle systematics.

Materials and Methods

Specimens were obtained in various stages of liquid preservation; most often in Pampel's preservative (Ekis 1977:6) (now Opitz). The internal reproductive organs of all available fluid preserved checkered beetles were examined. The specimens examined involved genera of all currently recognized Cleridae subfamilies. Sufficient taxa diverse fluid preserved specimens were available for credible outgroup comparisons. Within subfamily Clerinae multiple species studied involved the genera *Aphelocerus*, *Aulicus*, *Axina*, *Balcus*, *Calendyma*, *Caestron*, *Cardiostichus*, *Clerus*, *Colyphus*, *Dieropsis*, *Eleale*, *Enoclerus*, *Epiclines*, *Chilioclerus*, *Gyponyx*, *Natalis*, *Omadius*, *Opilo*, *Phlogistomorpha*, *Phlogistus*, *Placopterus*, *Priocera*, *Scrobiger*, *Stigmatium*, *Thanasimus*, *Trichodes*, *Trogodendron*, and *Zenithicola*.

The arrangement of species follows subfamilial designations proposed by Crowson (1964:302) and followed by Lawrence and Newton (1995:869).

Results and Discussion

Anatomical Overview of Internal Reproductive Organs. The results of the analysis involving specimens of the abovementioned clerine genera indicated characteristics of the internal reproductive organs as follows. All males studied have
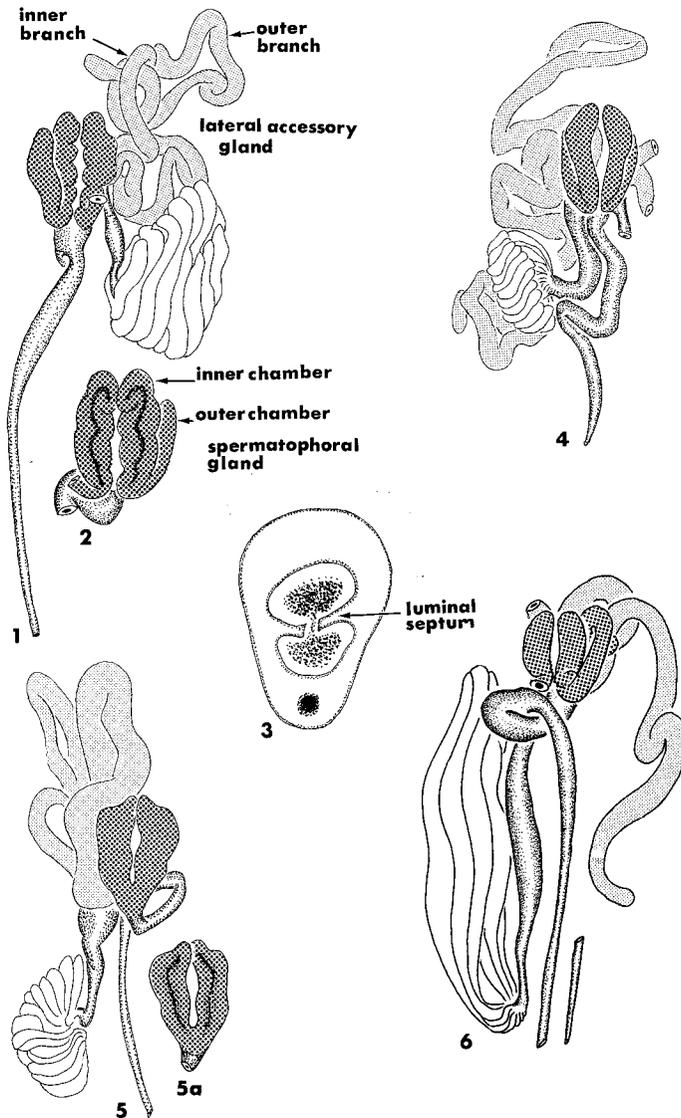
Figs. 1–6. Male reproductive organs. **1–3)** *Trichodes ornatus* (Say); **2)** spermatophore glands; **3)** cross-section of inner chamber of spermatophore gland; **4)** *Aulicus edwardsii* (Horn); **5–5a)** *Chilioclerus mimus* Solervicens; **5a)** spermatophore gland; **6)** *Opilo domesticus* (Sturm).

two pairs of accessory glands, with possible subdivision of the medial or lateral branches, or both. Spermatophoral glands (Fig. 2), associated with the "mating plug" type of spermatophore have been observed in the genera *Aulicus*, *Chilioclerus*, *Opilo*, *Scrobiger*, *Trichodes*, *Phlogistomorpha*, *Phlogistus*, *Trogodendron*, and *Zenithicola*. The seminal vesicle (Fig. 10) is bipartite in *Trogodendron rufipes* Elston. Also, in these
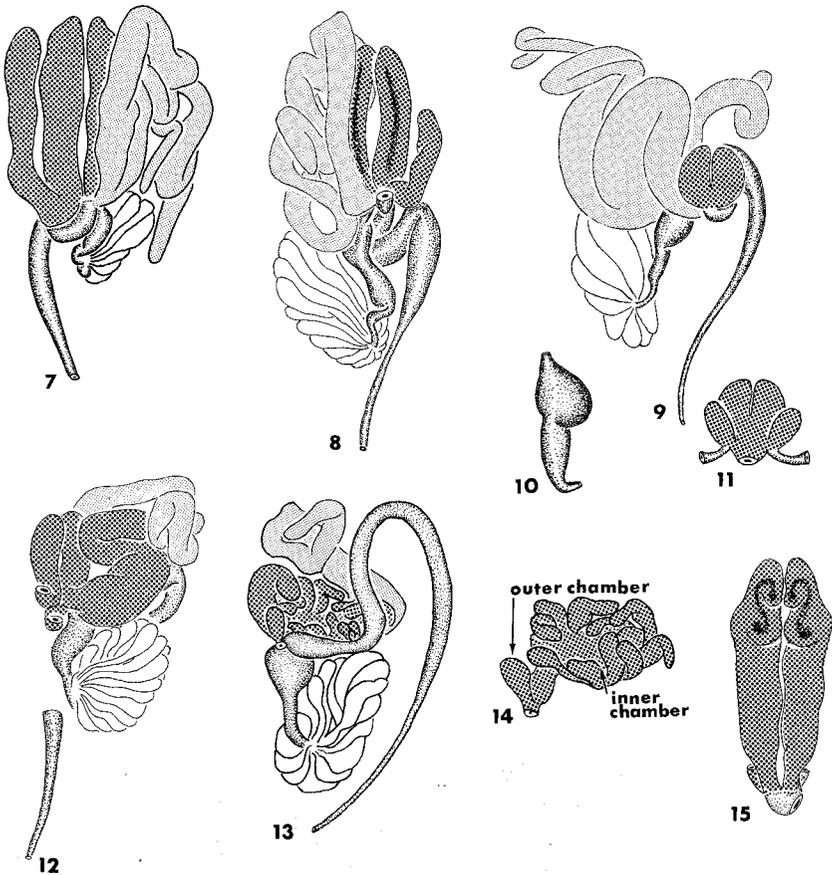
Figs. 7–15. Male reproductive organs. **7)** *Phlogistus imperialis* (Gorham), spermatophore gland; **8)** *Phlogistomorpha croesus* (Blackburn); **9–11)** *Trogodendron rufipes* Elston; **10)** seminal vesicle; **11)** spermatophore gland; **12)** *Zenithicola funestus* Chevrolat; **13–14)** *Scrobiger splendidus* (Newman); **14)** spermatophore gland; **15)** *Phlogistus imperialis* (Gorham), spermatophore gland.

genera, and in *Balcus* and *Dieropsis*, the spermathecal capsule is not capsular but divided into a primary and secondary chamber (Fig. 30), and the bursa copulatrix is absent or has been modified into a spermatophoral receptacle. In most of the other abovementioned genera the spermatheca is capsular and there is a distinctly formed saccular bursa copulatrix; the exceptions being in members of *Eleale* and *Priocera* in which the bursa copulatrix is also absent. A distinct spermathecal duct may or may not be present.

The pair of clerid accessory glands that evolved into the particular type of spermatophoral gland depicted herein (Fig. 2) has a bean-shaped configuation; a spermatophoral gland shape also found in Tenebrionidae (Grimes and Happ 1980:284). The walls of this gland are considerably thicker than the wall of the lateral accessory glands, with the inner chamber showing an incomplete luminal septum
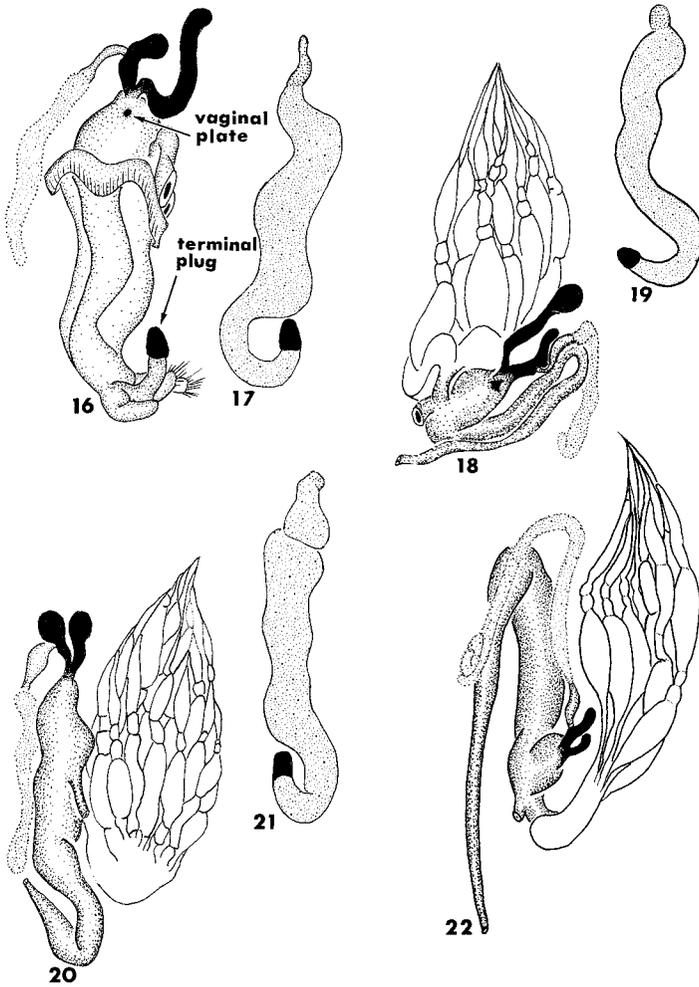
Figs. 16–22. Female reproductive organs. **16–17)** *Trichodes oregonensis* Barr; **16)** spermatophore *in situ*; **17)** spermatophore; **18)** *Trichodes ornatus* (Say); **19)** spermatophore; **20–21)** *Aulicus edwardsii* (Horn); **21)** spermatophore; **22)** *Opilo domesticus* (Sturm).

(Fig. 3). The inner chamber is usually short, feebly lobate, and reniform (Figs. 1–2, 4–6, 9, 12) or elongated and sinuous (Figs. 7, 8, 15). In *Scrobiger splendidus* (Newman) the inner chamber is highly diverticulated (Figs. 13–14), whereas the outer chamber is particularly short. In all species examined, except in *Chilioclerus mimus* Solervicens (Figs. 5–5a), the spermatophoral gland has an outer chamber that may be slightly shorter (Figs. 1–2, 4, 7, 8, 11) or longer (Figs. 6, 12) than the inner chamber. In *Trichodes*, *Chilioclerus*, *Phlogistomorpha*, and *Phlogistus* a dorsal view of the inner chamber (Fig. 2) shows a peculiar dark rod-like structure which when removed from the gland is comprised of a hard but pliable material whose composition is similar to that of the spermatophoral capsule and spermatophoral terminal plug (Fig. 16).
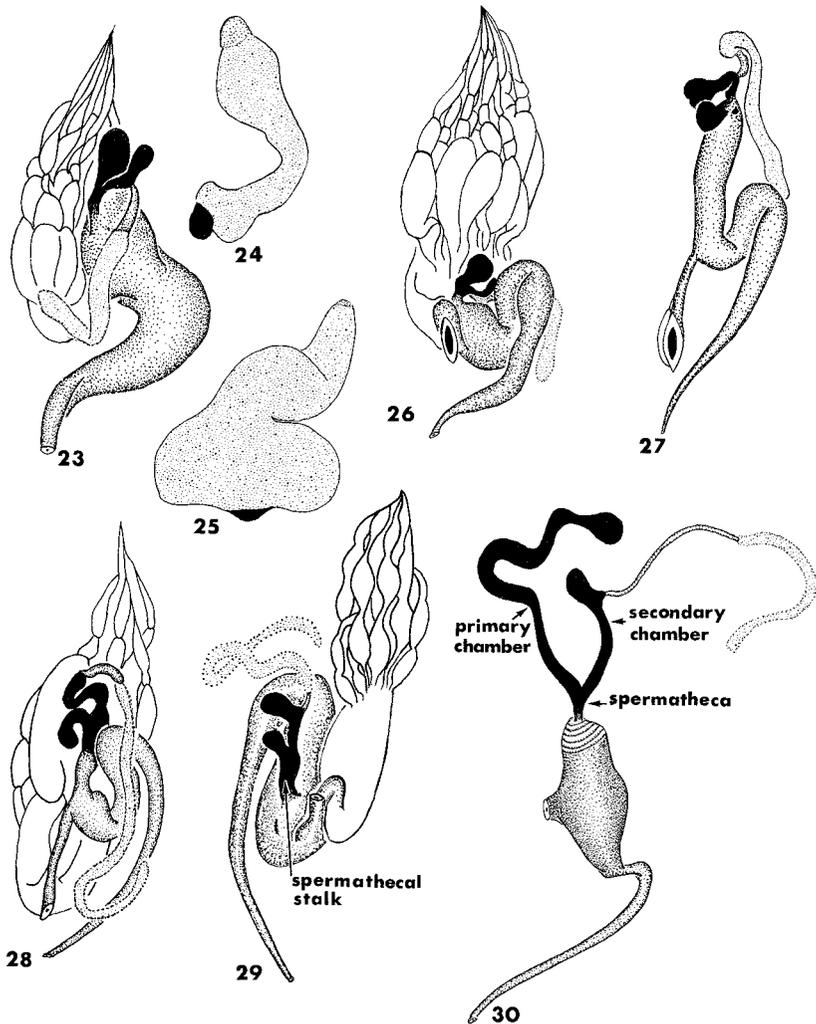
Figs. 23–30. Female reproductive organs. **23–24)** *Phlogistomorph croesus* (Blackburn); **24)** spermatophore; **25)** *Phlogistus imperialis* (Gorham) spermatophore; **26)** *Zenithicola funestus* Chevrolat; **27)** *Trogodendron fasciculatum* (Schreiber); **28)** *Scrobiger splendidus* (Newman); **29)** *Balcus signatus* Broun; **30)** *Dieropsis quadriplagiata* (Gorham).

Within Clerinae, an outstanding derived characteristic of the spermatophoral clerines is the manner into which the spermathecal capsule is divided into two chambers or branches. The primary chamber is most often longer and more robust (Figs. 16, 18, 23, 26, 30) than the secondary chamber to which the spermathecal gland is attached. In *Aulicus edwardsii* (Horn) the spermathecal chambers are about equal in size, but in *Opilo domesticus* (Sturm), *Trogodendron fasciculatum* (Schreiber), *Scrobiger splendidus* (Newman), and *Balcus signatus* Broun the secondary chamber is distinctly

more robust than the primary chamber. Near the base of the spermatheca one may find a pair of paralateral vaginal plates (Fig. 16).

Presumed Characteristics of Internal Reproductive Organs of Ancestral Cleridae. On the basis of outgroup comparisons involving the cleroid families Melyridae, Trogositidae, and Chaetosomatidae one may make the following conjectures regarding the anatomical components of the internal reproductive system of ancestral Cleridae. The male organs consisted of a pair of multifollicular testes, tubular vas deferens, distinctly formed unichambered seminal vesicle, one pair of accessory glands, and a highly muscular ejaculatory duct. The presence of a single pair of male accessory glands in Chaetosomatidae and Trogositidae, and in various clerid taxa, suggests that the widespread occurrence of a double pair of accessory glands in the Cleridae is synapomorphic. Moreover, the available data suggest that ancestral Cleridae used the spermatophore method of sperm transference. However, the structural features of the spermatophoral organs in the progenitor of Cleridae were probably more similar to those found in Thaneroclerinae and Tillinae in which the spermatophore is a less structurally complex spheroid mass of semen.

The spermatophore of the clerine genera under study is considerably more complex as are the organs that produce and contain them. Therefore, the clerine spermatophore is regarded as an advanced, or apomorphic, state of spermatophoral development and may at least conceptually bring the clerines, with such properties of sperm transference, into a monophlyletic assemblage. To date, cleroid accessory glands that may be identified with confidence as spermatophoral glands (*sensu* Parker 1970:543), have been found only in the Cleridae; in Thaneroclerinae, Tillinae, and in Clerinae. Whether the spermatophore method of sperm transference unite the aforementioned subfamilies into a monophyletic group remains to be seen. For the present all that can be stated with confidence is that within Cleridae two levels of spermatophore reproductive strategies exist with the clerine type being the more advanced. Moreover, the evolutionary significance of the spermatophore glands, and the spermatophore method of sperm transference, to the higher classification of superfamily Cleroidea cannot be ascertained until a greater representation of cleroid taxa are available and suitably preserved in fluid. A complete luminal septum of the spermatophoral gland is presumed synapomorphic for Thaneroclerinae, as is its subsequent reduced condition in Tillinae and Clerinae.

On the basis of overall parsimony, one may assume the following characteristics of internal organs of the females of ancestral Cleridae. The spermatheca was of a noncapsular type with minimal sclerotization and no definitive proximal border. The capsular type of spermatheca, has to date not been found elsewhere in Cleroidea, but it is sporadically found in Tillinae, widespread in Clerinae, always present in Hydnocerinae, Enopliinae, and in Korynetinae. I consider its presence in Tillinae an example of homoplasy whereas its widespread presence in the other aforementioned subfamilies is considered synapomorphic. Absence of a bursa copulatrix in Thaneroclerinae, most Tillinae, and particularly in Hydnocerinae, whose members apparently do not produce spermatophores, and in some genera of Clerinae which do, is interpreted as plesiomorphic. Its absence, at least among the spermatophoral species, is functionally correlated with the need for a more spacious spermatophoral chamber provided by the proximal expansion of the vagina. On each side of the female spermatophoral chamber there is a conspicuous sclerite, the vaginal plate (Fig. 16) which, in pair, function as a compression organ to expedite the relocation of the sperm, locked in the spermotophore, into the spermathecal chambers. These sclerotic plates are also present in non-clerine spermatophoral species such as *Cymatodera* and *Lecontella*, of subfamily Tillinae. I found the vaginal plates of *Cymatodera* and *Lecontella* females taxonomically significant at species level (Opitz, pers. obs.) whereas Jean Menier made

the same find in the genus *Phloiocopus* (Menier, pers. comm.). Presence of a distinct saccular bursa copulatrix in Trogositidae, Melyridae, and in most Clerinae, Epiphloeinae, Enopliinae, Tarsosteninae, and Korynetinae makes it problematic to assess the phylogenetic significance of this organ in the Cleridae. It is clear that a greater number of generically diverse species will have to be examined from the internal anatomy aspect before a reasonable evolutionary statement can be made about the various structural/functional conditions of the bursa copulatrix.

Spermatophores

The following references to beetle families follows the taxonomic order of Lawrence and Newton (1995:782).

In the Coleoptera, spermatophores have been reported in **Dytiscidae** (Blunck 1912:210; Wigglesworth 1950:470; Crowson 1981:402), **Carabidae** (Jeannel 1941:40; Tuzet 1977:302), **Cicindelidae** [subfamily of Carabidae in Lawrence and Newton (1995:782)], (Freitag *et al*. 1980:131; Obata and Hidaka 1987:603; Rodriguez 1998: 741; 1999:1), **Hydrophilidae** (Gundevia and Ramamurty 1977:476; Ryker 1995:88), **Ptiliidae** (Darby 1982:7), **Silphidae** (Neuner *et al*. 1996:78), **Staphylinidae** (Foster *et al*. 1998:35; Gack and Peschke 1994:231), **Scarabaeidae** (Cros 1924:102; Heymons 1930:553; Fiori 1953:441; Landa 1960:302, 1961:935; Halffter and Lopez G. 1977:209; Crowson, 1981:402; Barratt and Campbell 1982:261; Rosales and Martinez 1992:120), **Elateridae** (Crowson 1981:114; Zacharuk 1958:733), **Lampyridae** (Van der Reijden *et al*. 1997:1202), **Cantharidae** (Khalifa 1949:467), **Anobiidae** (Goulson *et al*. 1993:541), **Coccinellidae** (Fischer 1959:206; Obato and Hidaka 1987:603), **Tenebrionidae** (Cros 1924:100; Fiori 1953:440, 441(Alleculidae); Sinha 1953:133; Davey 1960:111; Happ and Happ 1970:443; Gadzama and Happ 1974:107; Happ and Happ 1975:254; Frenk and Happ 1976:891; Grimnes and Happ 1980:281; 1986:635; Dailey *et al*. 1980:289; Black *et al*. 1982:110; Brits 1982:239; Dailey and Happ 1983:139; Happ 1984:386; Cloudsley-Thomson and Constantinou 1985:155; Bloch *et al*. 1996:894; Carver *et al*. 1999:566), **Meloidae** (Cros 1924:101; Fiori 1953:441; Selander 1964:1053; Gerber *et al*. 1971:1595; Gerber and Church 1976:1595; Alcock and Hadley 1987:45), **Pyrochroidae** (Eisner *et al*. 1996:6500), **Chrysomelidae** (Khalifa 1949:467; Lew and Ball 1980:360), **Bruchidae** [subfamily of Chrysomelidae in Lawrence and Newton 1995:787] (Huignard 1969:2939; 1974:361; 1975a:14; 1975b:83; 1978:1301; 1983:56; Huignard and Lamy 1972:1067; Huignard *et al*. 1977:354; Boucher and Huignard 1987:950), **Curculionidae** (Khalifa 1949:467), **Scolytidae** (Cerezke 1964:489), and Kasap and Crowson (1975:449) and Gardner (1989:296) described spermatophoral glands in **Buprestoidea**, **Dryopoidea**, **Byrrhoidea**, **Elateroidea**, **Cantharoidea**, and **Dascilloidea**, and **Buprestidae**, respectively. Fiori (1954:390) designated tubuliform, "first degree" type of accessory glands as spermatophoral in **Carabidae**, **Cicindelidae**, **Dytiscidae**, and **Gyrinidae**.

Clerid spermatophores are of the "mating-plug" type (*sensu* Thornill and Alcock 1983:339) and in development correspond to the "first female-determined" type of Gerber (1970:359). During the mating act, the male transfers to his mate a considerable quantity of viscous semen, largely composed of secretions from the lateral accessory glands. The secretions fill the female reproductive tract, whose lumen determines spermatophoral form. Histological preparations confirmed that the products from the lateral accessory glands comprise the bulk of the spermatophore whereas those from the spermatophore glands produce the thin outer envelope and the terminal plug (Fig. 16). Thornill and Alcock (1983:339) have equated a mating-plug type of spermatophore with the concept of sperm competition and a form of male
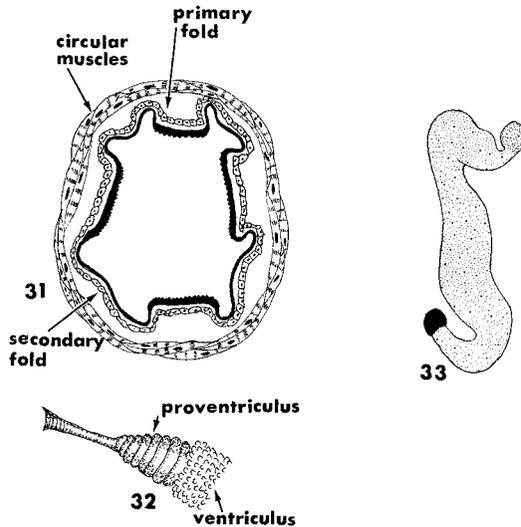
Figs. 31–33. Alimentary canal and spermatophore. **31–32)** *Trichodes ornatus* (Say). **31)** cross-section of proventriculus; **32)** stomodaeum and anterior portion of ventriculus; **33)** *Trichodes leucopsideus* (Olivier).

guarding. The proposal is that once a male has deposited the spermatophoral ingredients into the female the terminal plug, and the bulky spermatophore, prevents other males from inseminating the same female. The discovery of partially disorganized spermatophores in *Trichodes ornatus* (Say) females (Opitz, unpubl.) and other species suggests that in the Cleridae spermatophores are eventually metabolized and serve, in part, to nourish the female.

The Nutritional Value of Insect Spermatophores. The nutritional value of spermatophores to females has been verified in several orders of insects (Mann 1984:100; Kaulenas 1992:132), and particularly in Orthoptera (Friedel and Gillot 1977:147), Blattaria (Mullins and Keil 1980:567; Schal and Bell 1982:170), Lepidoptera (La Munyon and Eisner 1994:7081), Coleoptera (Landa 1960:308; Huignard 1983:62; Boucher and Huignard 1987:955; Cratsley 1997:112, van der Reijden, Monchamp, and Lewis 1997:1206; Rooney and Lewis 1999:102). For a general review and references see Anderson (1994:100) and Vahed (1998:59).

Spermatophores of the clerid genera *Trichodes* (Figs. 17, 19, 33), *Aulicus* (Fig. 21), *Phlogistus* (Fig. 25), and *Phlogistomorpha* (Fig. 24) have been extracted from females and examined. The sperm dose is concentrated in a small anterior region of the spermatophore whose main composition involves secretions from the lateral accessory glands. In view of their large mass, these spermatophores represent a substantial energy investment for the male, but whether this investment is intended to nourish females has not been chemically substantiated. However, when one compares the structural and histochemical characteristics of nutritive spermatophores of other beetles (Landa 1960:307; Gerber *et al.* 1971:1599) with the compositional characteristics of the clerine spermatophore, there is little doubt that the clerine spermatophore is highly proteinaceous and provides substantial nourishment to females. In the case of the anthophilous clerids, *i.e.,* those that produce spermatophores, the spermatophoral nutrients may well serve to fill a food void, an aspect of spermatophoral function

investigated by Gwynne and Simmons (1990:172) and Hinton (1964). As stated by Boucher and Huignard (1987:956), ''Male secretions contained in spermatophores can thus constitute a substantial trophic source, when food is unavailable, and can influence reproduction.'' I contend that male spermatophoral clerines produce highly nutritive spermatophores. This source of nutrition is used by females whose cycle of repro- duction must keep in synchrony with those environmental parameters required by the immature stages. Several of the clerines in question are known anthophiles and therefore are subjected to floral periodicity. Consequently the females of these species may at times be deprived of pollen and nectar, food resources, and mates, available for only brief, usually vernal times.

The development of a more spacious, biramous spermatheca and highly expanded vagina, characteristic of the abovementioned genera (Figs. 16, 18, 20, 22–23, 26–30), may be construed as adaptations for the reception of a large mass of nutritive se- cretions, and serves also to permit prolonged storage of an extraordinarily large dose of sperm. Such a strategy of insemination ensures availability of sperm to the female over an expanded period of time, at a time when the impetus for male and female aggregation, *i.e.,* flower resources, may be temporarily unpredictable, or at best phe- nologically sporadic. Simmons and Parker (1989:337) discussed correlation among frequency of mating, nutritional advantages from increased dosage of seminal fluid, and selection towards increased spermatophoral size.

Several genera of Cleridae implement spermatophores. As stated previously, there are basically two types of spermatophoral development in the Cleridae. There is ample indication that the shape of the clerine type of spermatophore is taxonomically significant at generic level, and, at least in *Trichodes*, the taxonomic significance seems to extend to species levels as well. Mann (1984:5) concluded that among invertebrates, ''spermatophores differ so much in size, shape, and structure between species that in many instances they can be used as reliable, species specific taxonomic markers.'' Similar comments were made by Petersen (1907) in his work on butterflies and moths.

Phylogenetic and Historical Biogeographic Implications
of Clerinae Spermatophores

An inherent variable in empirical assessments of character phylogeny is the question wether sufficient taxa are being considered during in-group and out-group comparisons. This is particularly a concern when the character states analysis involves the more delicate soft tissues of the internal reproductive organs. Properly fluid-preserved, and taxonomically diverse, specimens from global regions are very difficult to obtain. Therefore, the discussion that follows is offered as a tentative indication of relationship patterns that seem to be emerging from a world study of Cleridae internal anatomy. The intent of this work is not to propose a refutable phylogenetic discussion of spermatophoral Clerinae. However, some empirical information towards that goal can be presented as can, with considerable confidence, a short list of character states and table of character matrix.

Character and Character States Used in the Discussion. Nine adult morpho- logical characters of the spermatophoral clerines and species of Chaetosomatidae, Trogositidae, and Melyridae were used in the analysis (Table 1). Geographical representation of species involved North America, Central America, South America, Africa, Europe, and Australia. Character states designated as ''0'' are considered plesiomorphic whereas those given a value of ''1'' or ''2'' (involving a transformation series) are judged apomorphic.

Table 1. Character Matrix of eight morphological characters for 34 taxa.

| Taxa	Characters								
	1	2	3	4	5	6	7	8	9
Melyridae	0	0	0	0	0	0	1	0	0
Trogositidae	0	0	0	0	0	0	0	0	0
Chaetosomatidae	—	—	0	0	0	0	0	0	0
Thaneroclerinae	1	0	1	0	0	0	1	1	0
Tillinae	0	0&1	1	1	0	0	1	0	0
Hydnocerinae	1	0	0	0	1	1	0	0	0
Clerinae	0	0&2	0	0	0	0	1	0	0&1
Aulicus	0	1	2	0	0	0	1	0	1
Chilioclerus	—	—	2	0	0	0	1	0	0
Opilo	0	1	2	0	0	0	1	0	0
Scrobiger	0	1	2	0	0	0	1	0	1
Trichodes	0	1	2	0	0	0	1	0	1
Phlogistomorpha	0	1	2	0	0	0	1	0	1
Phlogistus	0	1	2	0	0	0	1	0	1
Trogodendron	0	1	2	0	0	0	1	0	1
Zenithicola	0	1	2	0	0	0	1	0	1
Balcus	0	1	2	—	—	—	—	—	0
Dieropsis	0	1	2	—	—	—	—	—	1
Aphelocerus	0	0	0	0	0	0	1	0	0
Axina	0	0	0	0	0	0	1	0	0
Calendyma	0	0	0	—	—	—	—	1	
Caestron	0	0	0	0	0	0	0	0	
Cardiostichus	0	0	0	0	0	0	0	0	
Clerus	0	0	0	0	0	0	0	0	
Colyphus	0	0	0	0	0	0	0	0	
Eleale	0	0	0	0	0	0	0	1	
Enoclerus	0	0	0	0	0	0	0	0	
Epiclines	0	0	0	0	0	0	0	0	
Gyponyx	0	0	0	—	—	—	—	—	
Metademius	0	0	0	—	—	—	—	—	
Omadius	0	0	0	0	0	0	0	0	
Placopterus	0	0	0	0	0	0	0	0	
Stigmatium	0	0	0	0	0	0	0	0	
Thanasimus	0	0	0	0	0	0	0	0	

1. Bursa copulatrix: (0) present; (1) absent
2. Spermathecae: (0) unbranched; (1) branched (Fig. 30)
3. Spermatophore: (0) absent; (1) not mating—plug type; (2) mating—plug type
4. Testis: (0) multifollicular; (1) unifollicular
5. Vas deferens   (0) narrow tubular; (1) not narrow tubular
6. Seminal vescicle: (0) unichambered; (1) multichambered
7. Male accessory
    gland: (0) one pair; (1) more than one pair
8. Luminal septum: (0) absent; (1) present (Fig. 3)
9. Peg sensilla: (0) absent or sparsely distributed; (1) profusely distributed
        (Fig. 49)

The configuration of the spermatophoral glands and/or of the spermathecae, found among several geographically widespread clerine genera, are so extraordinary in
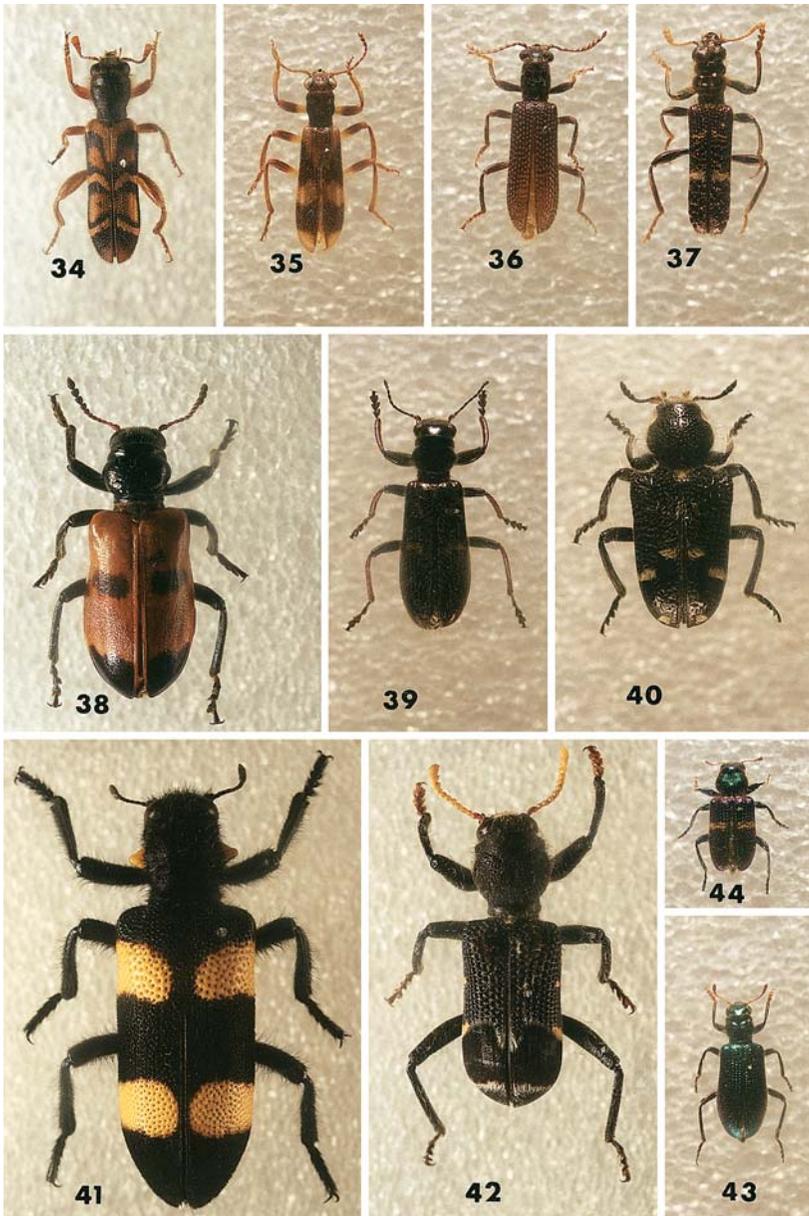
Figs. 34–44. Representative species of spermatophoral Clerinae. **34)** *Trichodes peninsularis* Horn; **35)** *Opilo domesticus* (Sturm); **36)** *Chilioclerus mimus* Solervicens; **37)** *Scrobiger splendidus* (Newman); **38)** *Aulicus edwardsii* (Horn); **39)** *Balcus signatus* Broun; **40)** *Zenithicola funestus* Chevrolat; **41)** *Dieropsis quadriplagiata* (Gorham); **42)** *Trogodendron fasciculatum* (Schreiber); **43)** *Phlogistus instabilis* (Newman); **44)** *Phlogistomorpha croesus* (Blackburn).
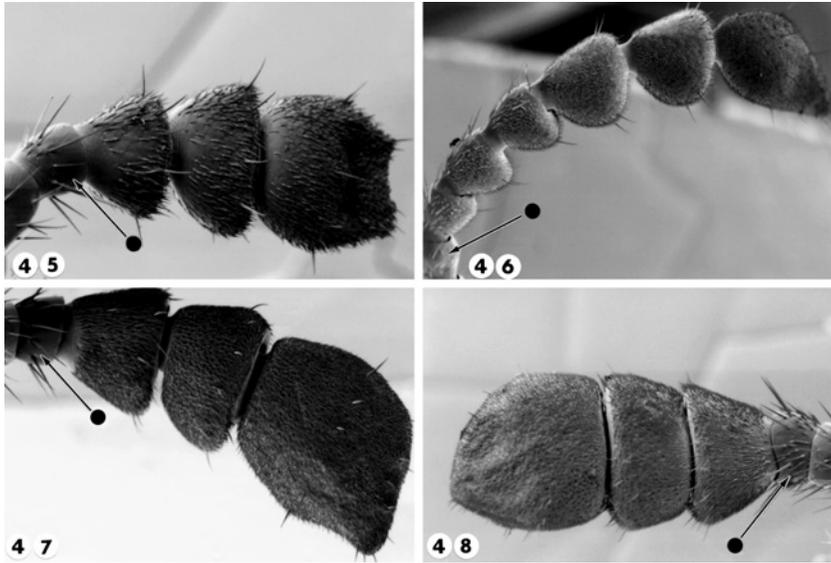
Figs. 45–48. Antennae of spermatophoral clerines. **45)** *Phlogistomorpha croesus* (Blackburn); **46)** *Aulicus antennatus* Schaeffer; **47)** *Zenithicola funestus* (Chevrolat); **48)** *Trichodes ornatus* Say.

development when compared to these organs of other Cleridae, that they invite speculation that the clerine genera in question form a close evolutionary grouping. However, their definitive association into a monophyletic group, or their placement into a separate taxonomic grouping must await a more taxa rich investigation of internal and external anatomy. Nevertheless, the complementarity among these genera in internal structure, particular type of antennal sensilla, and anthophilic life style, on the one hand, and extensive degree of divergence of external structure (Figs. 34–44), widespread geographic distribution, and pollenaceous life habits, on the other hand, suggests that they must have evolved from a common, but relatively ancient ancestral stock; perhaps from a Jurassic stem species.

Specimens of the following Clerinae genera show the type of anatomical features that is equated with production of the mating-plug type of spermatophore (Fig. 17): ***Aulicus*** (North America), ***Trichodes*** (North America, Eurasia, Africa), ***Chilioclerus*** (South America), ***Opilo*** (Eurasia, Africa, Australia), ***Diaropsis*** (Africa), ***Phlogistus*** (Australia), ***Phlogistomorpha*** (Australia), ***Zenithicola*** (Australia), ***Scrobiger*** (Australia), ***Trogodendron*** (Australia), and ***Balcus*** (New Zealand). It is too early to predict monophyletic status for this assemblage of genera, but it is likely that they must have undergone considerable anagenesis from the time of their initial divergence from a Gondwanan ancestor during, perhaps, Late Jurassic, some 152 million years ago. There is substantial gross integumental diversity among these genera. However, many share a peculiar microsensillar property of the terminal antennomeres (*e.g.,* see Figs. 45–54). The absence of these afferent organs on the proximal antennomeres provides a clear contrast of surface features of antennomeres as indicated in Figures 45–48, 53. In *Phlogistomorpha croesus* (Blackburn) (Figs. 45, 51), *Zenithicola funestus* (Chevrolat) (Figs. 47–52), *Dieropsis quadriplagiata* Gahan (Figs. 53, 54), and *Trichodes ornatus* Say
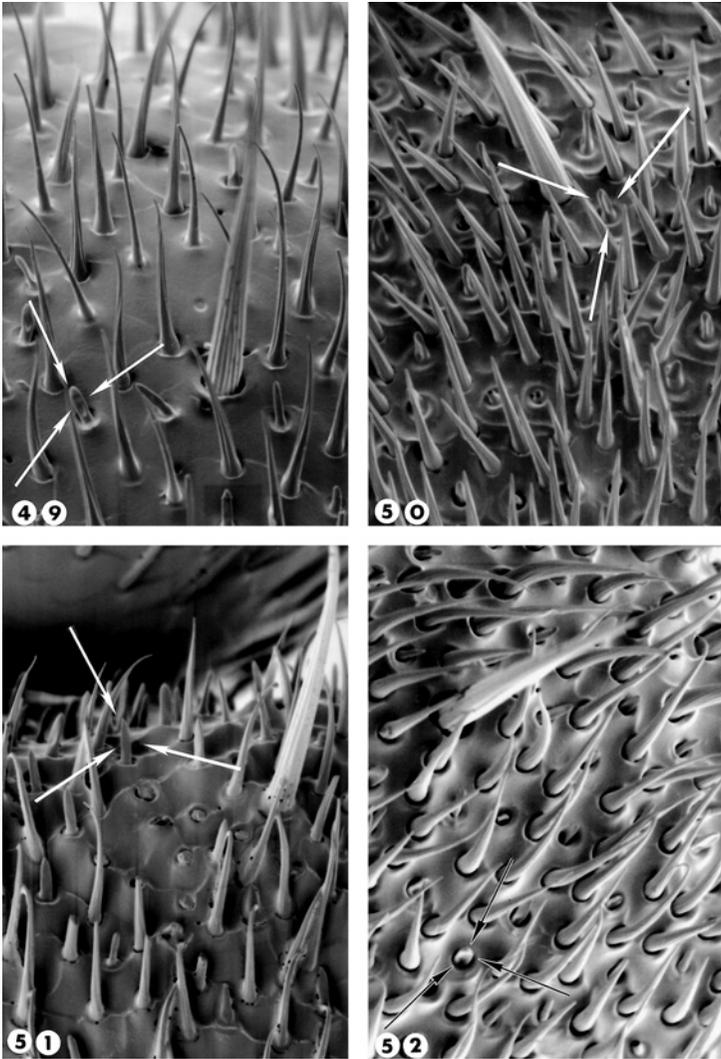
Figs. 49–52. Integumental sensilla on antennomere 10. **49)** *Aulicus antennatus* Schaeffer; **50)** *Trichodes ornatus* Say; **51)** *Phlogistomorpha croesus* (Blackburn); **52)** *Zenithicola funestus* Chevrolat.

(Figs. 48–50), these sensilla are found only on the last three antennomeres, whereas in *Aulicus antennatus* Schaeffer (Figs. 46, 49) they occur on the last six antennomeres.

Structurally similar sensillae, referred to as peg sensillae, are found in various other family of beetles. For example, on the antenna of the chrysomelid *Psylliodes chrysocephala* Linnaeus such afferent organs are known to have a combined olfactory thermoreceptive function (Bartlet *et al*. 1999:298 and references therein). Perhaps the antennal thermoreceptors in these clerids serve to detect thermal gradients that
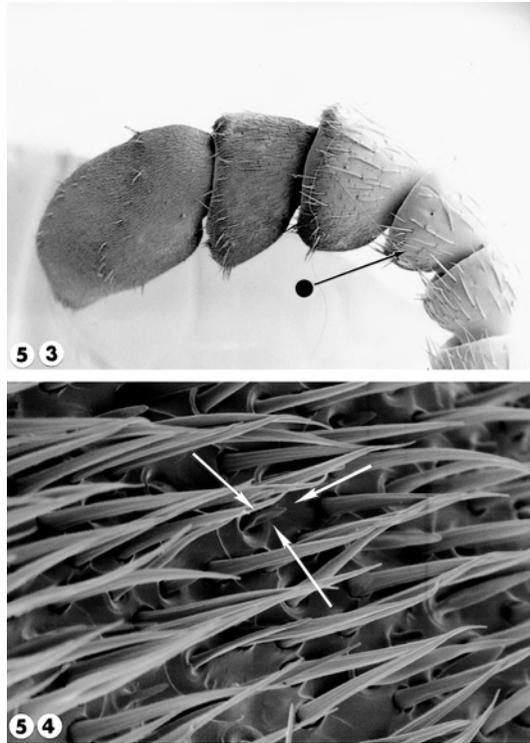
Figs. 53–54. Antenna of *Dieropsis quadriplagiata* Gahan. **53)** Antenna; **54)** sensilla of antennomere 10.

would be established during outbreaks of bush fires common in xeric environs; habitat of many of the beetles in question. Such thermoreceptor adaptations would form an important component of an escape mechanism involving flight from bush or forest fires.

The modern distribution of spermatophoral clerines (Fig. 55) invites an interpretation of evolutionary history that began with a stem species widespread when major ancient land masses were still relatively proximal to each other, *i.e.,* prior to any extensive drift of Laurasia from Gondwana. Moreover, many species of the species in question frequent flowers to obtain nutrition and to aggregate for mating. The anthophilic life style coupled with anatomical adaptation for pollen feeding suggests coevolution with ancient angiosperms. The early existence of an exine (outer cover of pollen grain) on ancient pollen, and perhaps a pollen protective device, suggests insect/pollen interactions during early angiosperm diversification (Brenner 1996:111). The earliest fossil record of such advanced pollen developments date to the Lower Cretaceous (Valanginian) some 132 million years ago (Brenner 1996:91) and provide a minimum estimate of the earliest likely insect/pollen interactions. It is widely believed that flower structure became modified as a coevolutionary process between flowers and pollinators.

If the progenitor of the abovementioned clerids had an anthophilic lifestyle, then I suggest their ancestral stock arose in western Gondwana, the inferred cradle of angiosperm evolution. Moreover, a Late Jurassic tectonic arrangement of continents
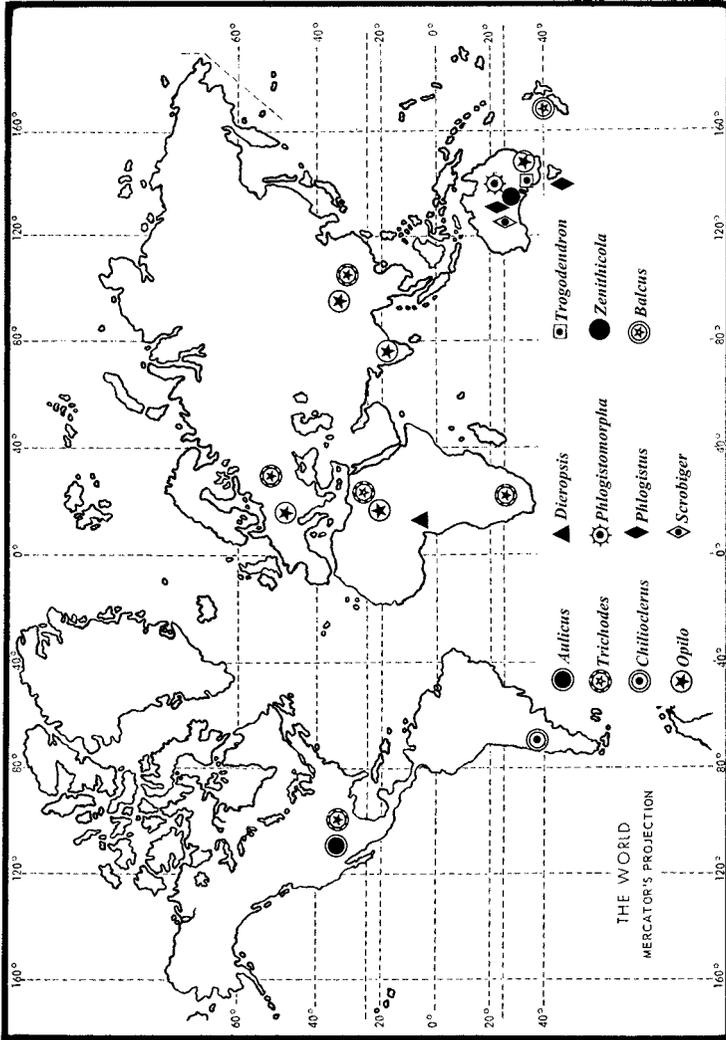
Fig. 55. General modern distribution of known spermatophoral genera of Clerinae.
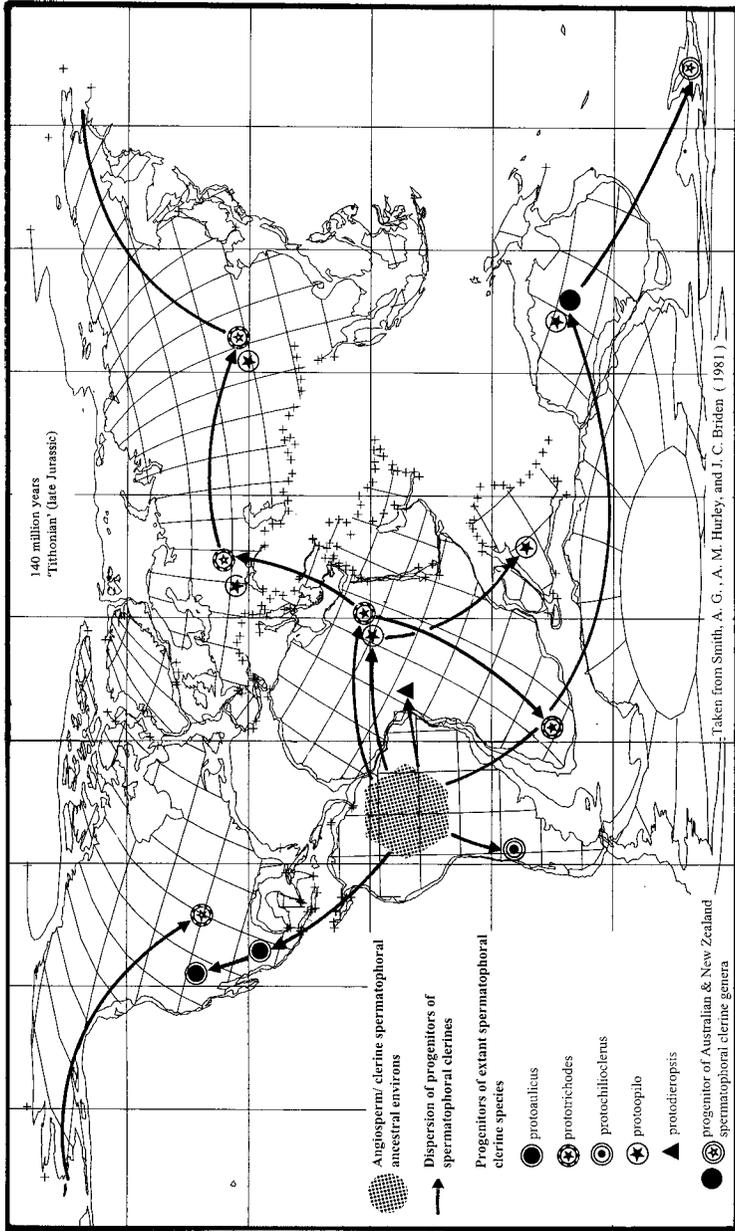
Fig. 56. A hypothesis of paleogeographic dispersal of progenitors of spermatophoral Clerinae.

provides plausible dispersal routes for the ancestral anthophilous clerines (Fig. 56). Support for a pre-Cretaceous origin of angiosperms has been brought forth from several fronts, from DNA analysis (Martin, Gieri, and Saedler 1989:48; Wolfe, Gouy, Yang, Sharp, and Li 1989:6205), from paleobotany (Cornet 1986:285), from paleoclimatography (Axelrod 1961:451; 1970:281), and from cladistic analysis (Doyle and Donoghue 1986:383; Crane 1985:783). Today, a belief is widely held that western Gondwana served as the ancestral region for the first angiosperms (White 1988:40). At some more recent time, possibly by the end of early Cretaceous (Albian, 112 million years ago) when angiosperms began to flourish, various components of this ancestral population of clerids became more geographically isolated, in part due to tectonic vicariance, to evolve into Laurasian and Gondwanan progenitors that produced our current, highly diverse, clerine spermatophoral genera.

Anthophily Among Spermatophoral Clerinae

The linking of these insects to angiosperm radiation is based on the current association of several of the genera with flowering plants and on the elaborate structural adaptations of their alimentary canal (crushing plates of the proventriculus) and internal reproductive organs; presumed structural manifestations resulting from evolution toward anthophily. The majority of species that belong to these speciose genera have been collected on flowers. Pollen feeding habits have been confirmed in *Trichodes* (Linsley 1936:257; Linsley and MacSwain 1943:598; Foster 1976:65; Balduf 1935:107) and flower visitations have been reported for *Aulicus* (Barr and Foster 1979:1). Collection label information, reports from naturalists, and personal observations confirm that flowers are also visited by individuals of *Phlogistus*, *Odontophlogistus*, *Trogodendron*, and *Zenithicola*.

Ekis and Gupta (1971:80) investigated the digestive system of Cleridae and found the intima of the primary proventricular folds of *Trichodes* particularly robust and minutely denticulate (Fig. 31), and the proventricular musculature prominent (Fig. 32). Undoubtedly these attributes represent adaptations for the physical breakdown of pollen grains frequently found in the lumen of proventriculi of *Trichodes* species (Opitz, pers. obs.).

Beetles may have been among the first pollinators of gymnosperms (Crowson 1981:599) and of angiosperms (Friis *et al.* 1986:194; Pellmyr and Thieu 1986:77). Crepet *et al.* (1991:191) reviewed the fossil evidence of early anthophilous beetles from the early Jurassic and late Cretaceous. Further, the fossil record indicates considerable parallel radiation of angiosperms and anthophilous insect taxa (Pellmyr 1992:46). If the early ancestor of the spermatophoral clerines became associated with incipient angiosperms, and subsequently perfected an anthophilous character as plants became more elaborate in flower structure and phenology, then the road to anthophily may help explain the evolution and adaptive significance of their atypical organs of reproduction and spermatophore method of sperm transference. The hypothesis is that the nutritional function of the spermatophore, particularly relevant when "flower food" is scarce, coevolved with the anthophilic character of the ancestral stock of spermatophoral clerines.

Conclusions

Variations among the internal organs, and particularly those of the reproductive organs, within Cleridae are potentially a vast source of phylogenetically significant character states. Crowson (1972:339) was the first to make such an assessment in his

interpretations of the systematic value of the alimentary canal in Cleridae. The number of pairs of the male accessory glands, and their structural characteristics, appear significant at familial and subfamilial levels. Subdivision of the male accessory glands (Ekis 1978), presence or absence of vaginal plates (Fig. 16), and attachment sites of the spermathecal gland show potential for significance at infra-generic–suprageneric levels. The follicular composition of the testis of examined Tillinae sets apart two groups of genera, those with unifollicular testes and those with multifollicular testes; the multifollicular condition is presumed synapomorphic. Some structural variation of the spermatheca, and presence or absence of a definitive bursa copulatrix, appear to be evolutionarily significant at the interfamilial and subfamilial levels.

The spermatophoral glands and spermathecal structure among morphologically diverse clerine genera, and the widespread geographical distribution of these generic groups, suggest an ancient common ancestry dating to a geologic time when Laurasia was still relatively proximal to Gondwana. The evolution and diversification of the spermatophoral clerines are probably linked to ancient angiosperm proliferations and, at least among the extant species, to modern angiosperm flowering patterns. Anthophily, which characterizes many of the genera in question, suggests a coevolution with angiosperms. Flowering plants are believed to have radiated throughout Gondwana and north to Laurasia (White 1988:40) and presumably so did the ancestors of an ancient stock of anthophilous clerids that produced these morphologically diverse extant groups of clerines (Figs. 34–44).

Fluid preserved specimens representing a greater inventory of taxa need to be studied to expand, modify, and generally contribute to the refinement of our knowledge of clerid evolution.

Acknowledgments

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