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THE FAMILY IURIDAE THORELL (ARACHNIDA, SCORPIONES)

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ABSTRACT

The phylogenetic relationships of some chactoid genera are analyzed. The number of lateral eyes, the only character used to separate the families Chactidae and Vaejovidae, is rejected because of considerable intrageneric, intergeneric, and interfamilial variability. The value of trichobothrial numbers and patterns in scorpion systematics is discussed, and the terminologies proposed by both Stahnke and Vachon are considered to be of limited value in phylogeny reconstruction because they postulate incongruent homologies. The following sister-group relationships and monophyletic taxa are hypothesized: *Caraboctonus* + *Hadruroides* = Caraboctonini, new; *Hadrurus* = Hadrurini, new; Caraboctonini + Hadrurini = Caraboctoninae; *Calchas* + *Iurus* = Iurinae; Caraboctoninae + Iurinae = Iuridae, new rank. A key to scorpion families, and a key to subordinate taxa of Iuridae are presented. The suprageneric taxa of iurids are diagnosed and compared. A vicariance model is presented to explain the present geographical distribution of the family.

INTRODUCTION

"Considering the wide geographical range of this group [Iurini]and the difference of aspect presented by such of its members as *Scorpiops* and *Hadrurus*, one would be inclined to think the assemblage an unnatural one. But the intermediate forms that exist seem to show that this is not the case. For instance, from *Scorpiops* to *Iurus* is not a great leap; and similarly we can proceed from *Iurus* through *Uroctonus* and *Anuroctonus* to *Vejovis*, or through *Hadruroides* and *Caraboctonus* to *Hadrurus*. *Hadrurus* undoubtedly differs very much from *Iurus*, but no one will probably dispute that it is nearly allied to *Caraboctonus*; and the similarity that obtains between *Caraboctonus* and *Iurus* with respect to armature of the mandible, the hairy clothing of the soles of the feet, &c., may surely, when taken in conjuction with the other features already pointed out as characteristic of the Iurini, point to real kinship between the two."

Pocock 1893:309

Pocock's (1893) subfamily Iurini (*sic*), its characterization and its included genera, represent (with additional genera described since) what is known as the family Vaejovidae of recent authors (cf. Stahnke 1974). Considerable evidence, however, clearly indicates that "the assemblage is an unnatural one." Some of that evidence and the taxonomic changes dictated by it are given below.

The genera discussed by Pocock and whose relationships form the central theme of this contribution presently constitute three distinct subfamilies within the Vaejovidae: *Caraboctonus* Pocock and *Hadruroides* Pocock make up the Caraboctoninae Kraepelin, *Hadrurus* Thorell and *Anuroctonus* Pocock form the Hadrurinae Stahnke, and *Iurus* Thorell constitutes the monogeneric Iurinae Thorell.

To complicate matters further, the chactid *Calchas* Birula must also be considered, for as Vachon (1971:718) indicates: "La trichobothriotaxie, la denture des chélicères diffèrent beaucoup de celles que l'on retrouve chez les autres Chactidae, ce qui prouve l'originalité de cette sous-famille (Calchinae Birula) à l'intérieur des Chactidae. Par contre ces caractères sont identiques à ceux possédés par le genre *Iurus* Thorell, appartenant à la famille des Vejovidae . . ." Thus, the relationships of four subfamilies (in two different families) are examined in this contribution.

Cladistic arguments are presented whenever possible. Seven Recent families of scorpions are currently recognized. The family Buthidae is apparently monophyletic based on trichobothrial patterns (Vachon 1974), cheliceral dentition (Vachon 1963), and male and female reproductive systems (Francke 1979), and may be the sister group of all the other Recent scorpion families (see also Lamoral 1980). The monogeneric Chaerilidae is monophyletic based on the trichobothrial pattern (Vachon 1974), chelicerae (Vachon 1963), and gnathobase morphology. Based on the male and female reproductive systems it appears that the Chaerilidae represent the sister-group of the remaining five Recent families. The superfamily Scorpionoidea (Diplocentridae plus Scorpionidae) appears monophyletic (with the exclusion of one genus perhaps) based on the female reproductive system and method of embryonic nutrition. The family Bothriuridae, classified by some in its own superfamily and by others in the Chactoidea, also appears monophyletic based on the female reproductive system, sternum shape, and venom gland morphology. Finally, the families Chactidae and Vaejovidae are here not considered to be monophyletic, although as a higher taxon (superfamily Chactoidea) they might be.

The families Chactidae and Vaejovidae are separated only by the number of lateral eyes: Chactidae with two pairs and Vaejovidae with three. This character, however, is known to be unreliable. Among "chactids" *Broteochactas* Pocock and *Teuthraustes* Simon actually have three or four pairs, *Broteas* Koch has two, three or four pairs, and *Chactopsis* Kraepelin has three pairs (Gonzales 1977); and the Typhlochactini Mitchell has five eyeless species in two genera (Francke 1981). Among "vaejovids" there is also considerable variability (Gertsch and Soleglad 1972); *Anuroctonus* has four pairs, and *Parascorpiops* Banks has two pairs (Francke 1976). This variability has resulted in considerable taxonomic confusion over the years: for example, the genus *Uroctonoides* Chamberlin was described as a vaejovid and subsequently shown to be a junior synonym of the chactid *Teuthraustes* (Soleglad 1973); and the genus *Chaerilomma* Roewer was described as a chactid and later shown to be a junior synonym of the vaejovid *Iurus* (Vachon 1966). The chaos in classification resulting from the use of this unreliable character is such that taxonomists must often identify the genus first, and then find out to which family it is assigned.

The phylogenetic relationships of chactoid scorpions can only be understood after monophyletic taxa are recognized, and the sister-group relationships among them figured out. Consequently, outgroup comparisons for this study were extremely difficult, as the level of generality of a given character was nearly impossible to determine. Comparisons are made within (a) the chactoids, (b) chactoids and bothriurids, (c) chactoids, bothriurids, and scorpionoids, (d) all non-buthid Recent scorpions, and finally (e) among all Recent scorpions. The postulated polarity of the transformation series can thus be correct at one level of generalization, and incorrect at another; only future studies will tell.

The aim of this contribution (and others in preparation) is to hypothesize monophyletic groupings within the chactoids: (a) by showing that previous hypotheses are not supported by the data available, and (b) by identifying shared derived characters (= synapomorphies) defining some chactoid elements.

PHYLOGENETIC RELATIONSHIPS

The relationships of *Caraboctonus* and *Hadruroides*.—The genus *Caraboctonus* contains a single species, *C. keyserlingi* Pocock, from central Chile, and *Hadruroides* contains seven species from Peru and Ecuador, including the Galapagos Islands (Maury 1975, Francke and Soleglad 1980). These two genera share a number of unique features which corroborate their hypothesized sister-group relationship (by being the only two genera placed in the Caraboctoninae). The most significant synapomorphies, based on outgroup comparisons with all Recent scorpions, are the trichobothrial patterns (Vachon 1974, Maury 1975), and the lack of a well developed ventral median claw (= unguicular spine) on the tarsus.

The dentition pattern on the pedipalp chela fingers is basically the same on both genera, with six (fixed finger) or seven (movable finger) distinct oblique rows. *Hadruroides* differs from *Caraboctonus*, however, in the presence of internal and external supernumerary granules flanking the oblique rows of principal granules. The supernumerary granules appear gradually after the third or fourth molts, and are absent on all other Recent scorpions with similar dentition patterns (i.e., six or seven distinct oblique rows). Thus, by outgroup comparison and by ontogenetic arguments (Nelson 1978), supernumerary granules are autapomorphic for *Hadruroides*.

The sternum can be about as long as wide with a deep longitudinal furrow in *Hadruroides*, or much wider than long and at most with a deep pit posteriorly and no furrow in *Caraboctonus*. Among chactoids the sternum is usually as long as wide with a longitudinal furrow. Therefore, the character state in *Caraboctonus* is hypothesized, by outgroup comparison, to represent an autapomorphy.

The relationships of *Anuroctonus* and *Hadrurus*.—Stahnke (1974) included only *Hadrurus*, with eight species, and *Anuroctonus*, with one species, in the subfamily Hadrurinae Stahnke. "This subfamily [Hadrurinae] is primarily characterized by its large number of trichobothria (86 to 145) as compared with all the other subfamilies [of Vaejovidae] (45 to 63) . . . Although the two genera assigned to this subfamily vary widely in some respects, the trichobothria indicate a closer affinity between them than to the genera herein assigned to the Vaejovinae" (Stahnke 1974:116, 118). The implied hypothesis is clear: these two genera are more closely related to each other than either is to any other Recent scorpion. The validity of this hypothesis is examined next.

TRICHOBOTHRIAL NUMBERS. Stahnke's use of absolute trichobothrial numbers on the pedipalp chela and tibia to characterize the Hadrurinae is somewhat superficial and vague. First, if Stahnke (1974, table 1, p. 121) used trichobothrial numbers as a measure of phenetic distance, we observe that he characterizes *Hadrurus* as having 145 trichobothria and *Anuroctonus* as having 86, a difference of 59. *Scorpiops* Peters varies from 53 to 64 trichobothria, a minimal difference of only 22 with respect to *Anuroctonus*. Phenetically at least, it would seem that *Anuroctonus* is closer to *Scorpiops* than either is to *Hadrurus*. Second, we might consider that Stahnke implied a cladistic interpretation, i.e., that the increase in trichobothrial count (to 86 or higher) is a synapomorphy. The genus *Dasyscorpiops* Vachon (Vaejovidae, Scorpiopsinae), recently described from Malacca, has 112 trichobothria (Vachon 1974). Cladistically, however, *Dasyscorpiops* is closer to *Scorpiops* than it is to either *Anuroctonus* or *Hadrurus* (based on cheliceral dentition, pedipalp finger dentition, carapace shape, and trichobothrial pattern). Therefore, a mere increase in trichobothrial numbers (to 86 or higher) does not necessarily represent a synapomorphy among vaejovids.

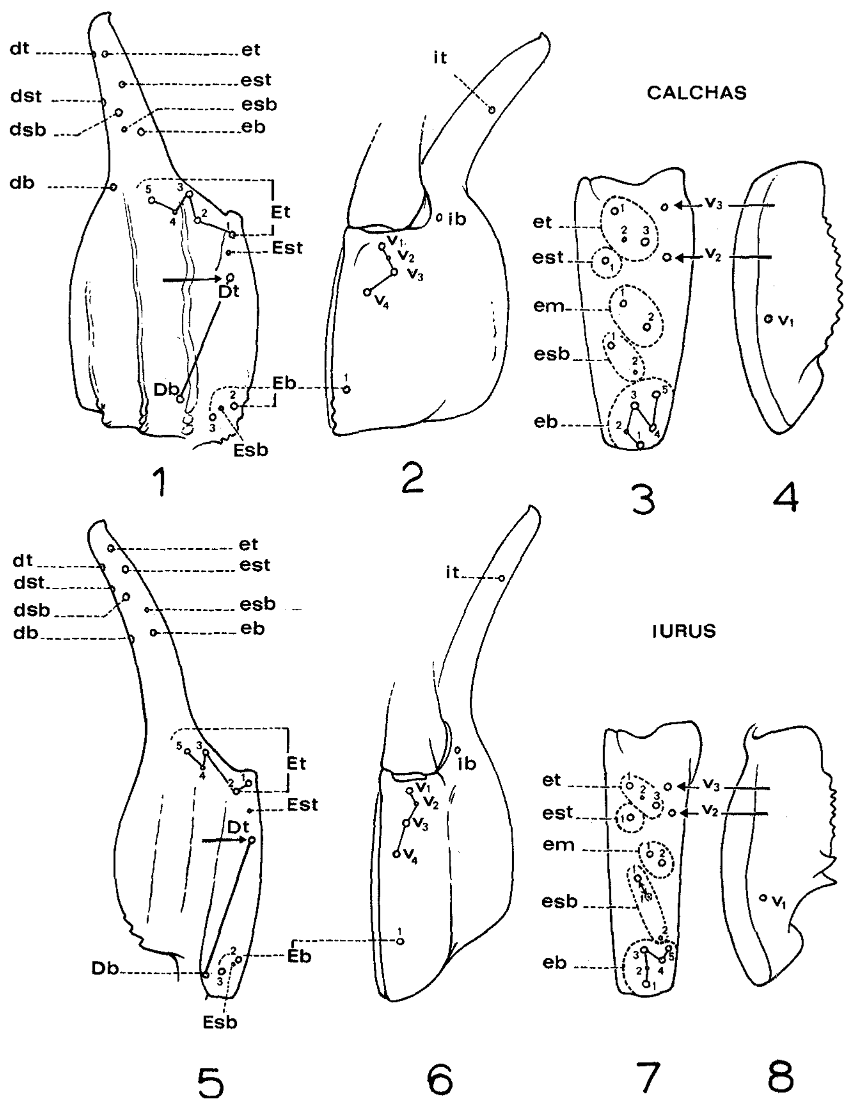
Next we might examine which regions of the pedipalps bear "larger than average numbers" of trichobothria in *Hadrurus* and *Anuroctonus* with respect to other vaejovids. These regions are the ventral aspect of the chela, and the external and ventral aspects of the tibia. Among vaejovids, all members of the subfamily Scorpiopsinae have "supernumerary" trichobothria on the external and ventral aspects of the tibia, and some *Scorpiops* also have them on the chela (Vachon 1974); *Uroctonus bogerti* Gertsch and Soleglad (Vaejovinae) and *Paravaejovis pumilis* (Williams) (Vaejovinae) have them on the ventral aspect of the chela. Thus, *Hadrurus* and *Anuroctonus* are not unique among vaejovids in this respect. As a matter of fact, according to Vachon (1974, table 4, pp. 935-936), "supernumerary" trichobothria occur in over 50% of the non-buthid genera studied by him. The presence of "supernumeraries" on both the tibia and chela occur in three genera of Bothriuridae, one genus of Chactidae, and seven genera of Scorpionidae, in addition to the vaejovids under consideration.

Therefore, regardless of whether we examine Stahnke's use of trichobothrial numbers phenetically or cladistically, and in the latter case whether we examine total or regionalized counts, the data do not offer strong support of the hypothesized sister-group relationship between *Anuroctonus* and *Hadrurus*.

TRICHOBOTHRIAL PATTERNS. Vachon (1972, 1974) has indicated that close examination of the positions of individual trichobothria is a more fruitful approach to the study of phylogenetic relationship in scorpions than merely counting them. Particularly interesting and relevant for this contribution are his illustrations of the patterns in *Iurus* and *Calchas*, reproduced in Figs. 1-8.

Two systems of trichobothrial nomenclature in scorpions are in use, Vachon's (1974) and Stahnke's (used in various publications; for the present discussion reference is make to his 1974 contribution on vaejovids). Unfortunately both systems sometimes generalize unnecessarily in their attempt to find "universal" patterns, and therefore sometimes use the same designation for non-homologous trichobothria or different designations for homologous ones.

Vachon (1974) recognized three "universal" patterns among scorpions. Pattern "A" for the Buthidae, "B" for Chaerilidae, and "C" for all other Recent families. These patterns are characterized by a given number of trichobothria on the femur, tibia, and chela of the pedipalps; the "universal" or "fundamental" number he termed orthobothriotaxia, and deviations from this number are designated neobothriotaxia (the evolutionary implications of this terminology are of no concern here). Deviations resulting in a greater number of trichobothria are termed "additive neobothriotaxia" (*neobothriotaxie majorante*), and decreases are "substractive neobothriotaxia" (*neobothriotaxie minorante*). Of 55 genera with pattern "C" examined by Vachon, only 26 (47%) are orthobothriotaxic, and 29 (53%) have additive neobothriotaxia. Thus, the "universality" of orthobothriotaxia "C" should be questioned on this basis alone. Cladistic hypotheses that orthobothriotaxia "C", established on the basis of absolute numbers, is either apomorphic or plesiomorphic are rejected because the patterns (i.e., the relative positions of the trichobothria) differ considerably between groups. It is important to note, however, that trichobothria can be gained or lost, and the direction of evolutionary change (i.e., the



Figs. 1-8.–Trichobothrial patterns of *Calchas* Birula (Chactidae) and *Iurus* Thorell (Vaejovidae): 1-4, *Calchas*; 5-8, *Iurus*. 1, 5, external aspect of pedipalp chela; 2, 6, ventrointernal aspect of chela; 3, 7, external aspect of pedipalp tibia; 4, 8, ventral aspect of tibia (from Vachon 1974).

polarity of the transformation series) must be empirically established for each taxon (see Francke 1981).

The trichobothrial patterns of the chela of *Hadruroides lunatus* (Koch), *Hadrurus pinteri* Stahnke, *Anuroctonus phaiodactylus* (Wood), and *Iurus dufoureius* (Brullé), with some of the homologies postulated by Vachon (1974) and Stahnke (1974) are shown in Figs. 9-16. In Vachon's scheme (Figs. 9-12), trichobothria ***Db-Dt*** are on the external aspect of the fixed finger in *Hadruroides* and *Caraboctonus*, basally on the dorsoexternal aspect of the palm in *Hadrurus* and *Anuroctonus*, and ***Dt*** is distally on the external aspect of the palm in *Iurus*. Since other vaejovid genera, such as *Uroctonus* Thorell, *Scorpiops* Peters, and *Vaejovis* Koch, have trichobothria ***Db-Dt*** basally on the palm, Vachon (1974:898) explains the condition observed in *Hadruroides* and *Caraboctonus* as being the result of "phylogenetic displacement" (or "emigration" in short form): "Nous pouvons logiquement admettre ces déplacements puisque lesdites trichobothries son absentes à la base de la main et qu'il en existe 2 de plus sur le doigt fixe."

Stahnke's scheme (Figs. 13-16) also implies considerable trichobothrial movement, the origin of which is never addressed. Trichobothrium I_2 is dorsally on the base of the fixed finger on *Caraboctonus* and *Hadruroides* and *Hadrurus*, is nonexistant on *Anuroctonus*, and occurs distally on the internal aspect of the finger in *Iurus*.

Comparing the patterns of *Iurus* and *Calchas* (Figs. 1-8), one observes a more credible form of trichobothrial displacement; namely, that the trichobothria on the finger are rather equidistant on both genera, but on *Calchas* they cover most of the finger while on *Iurus* they cover the distal one-half to two-thirds of the finger only. In this instance, allometric growth of the base of the finger of *Iurus* could account for differences observed.

The mechanism(s) whereby trichobothria can "emigrate" is left unexplained by both Vachon and Stahnke. Trichobothria are mechanoreceptors innervated by a single bipolar neuron each, and any mechanism proposed to account for trichobothrial migration must also adquately explain the migration of their respective neurons.

Indiscriminate migration of trichobothria is one possible explanation, albeit a rather unconvincing one, for the existence of certain preconceived patterns. An alternative explanation is that there are no "universal" patterns and that trichobothrial migration is minimal at best. We hypothesize that trichobothria occupying similar positions are homologous, and that discrepancies in Vachon's and Stahnke's topologies (determined in large part by their terminologies) are due to gain or loss of trichobothria either by suppression of trichobothrial development, by the development of a different type of sensory seta in that position, or by some other means (see Francke 1981).

There is no evidence of trichobothrial migration, and the alleged displacements may merely reflect the shortcomings of the terminologies developed by Vachon and Stahnke, respectively. Evidence of trichobothrial gain or loss is widespread. First, at the individual level it is not uncommon to find asymmetrical specimens with an "aberrant" number of trichobothria on one pedipalp (Maury 1973, Vachon 1975). These "aberrations" involve the loss of one or more trichobothria in some cases, the gain of trichobothria in others, and in many instances it is difficult to determine the direction of change. Second, at the species level considerable variability exists among taxa with "additive neobothriotaxia." Excellent examples are found in the chactids *Euscorpius* spp. (Curcić 1972, Vachon 1975, Valle 1975) and *Megacormus* spp. (Soleglad 1976a), bothriurids *Brachistosternus* spp. (Maury 1973), scorpionids *Urodacus* spp. (Koch 1977), and vaejovids *Hadrurus* spp. (Soleglad 1976b). Third, at the generic level considerable variability is also found among closely related species. The five genera cited above, considered monophyletic by most workers, are excellent examples. Soleglad's (1976b) work on *Hadrurus* is particularly relevant to this contribution: some species have no "accessory" (= supernumerary ?) trichobothria on the chela, some have them on the internal aspect of the fixed finger base, still others have them on the external aspect of the palm, and some even have them on both areas. Noteworthy is *Hadrurus pinteri* Stahnke, which has an "accessory" trichobothrium on the external aspect of the pedipalp finger (its significance will be discussed later).

Why, then, are authors reluctant to consider trichobothrial gain or loss as an alternative explanation to "migration" in their search for homologies between genera? Thus, according to Vachon (Figs. 9-12) trichobothrium ***Dt***, located submedially on the dorsal aspect of the palm in *Hadrurus*, has migrated (with its "companion" ***Db***) to a submedian position on the external aspect of the finger in *Hadruroides*, and to a subdistal position on the external aspect of the palm in *Iurus*. We find this hypothesis entirely unparsimonious: *Hadrurus pinteri* and *Hadruroides* plus *Caraboctonus* have ***six*** trichobothria on the external aspect of the finger, and these we consider homologous; the differences observed on the dorsal aspect of the palm are due to gain or loss of trichobothria in either taxon (once sister groups relationships are established for the taxa in question, cladistic methods can be used to formulate hypotheses about the direction of change). Likewise, as indicated above some *Hadrurus* species have "accessory" trichobothria on the external aspect of the palm, and the position of one of these corresponds very well with the position of ***Dt*** in *Iurus*, and is hence presumably homologous to ***Dt***.

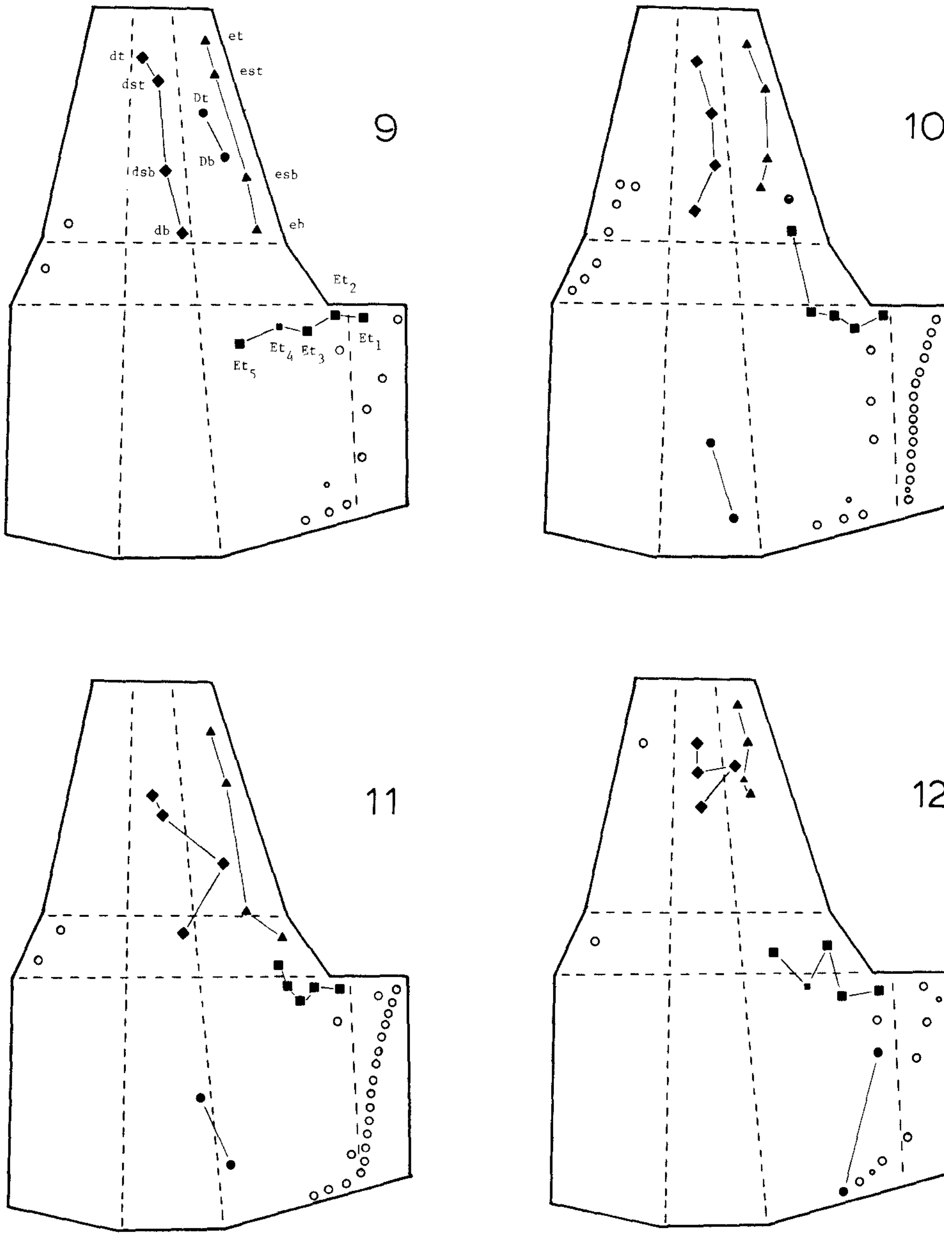
The shortcomings of Vachon's terminology are illustrated by the fact that trichobothrium ***Db*** in *Hadruroides* and *Caraboctonus* is in the same position as ***eb*** in *Hadrurus*, and ***dsb*** in *Anuroctonus* (Fig. 9-12). Stahnke's termonology is not much better: positionally, M_2 in *Hadruroides* and *Caraboctonus* = M_1 in *Hadrurus* = D_6 in *Anuroctonus*, and M_1 in *Hadruroides* and *Caraboctonus* = I_2 in *Hadrurus* = D_4 in *Anuroctonus* (Figs. 13-16).

In conclusion, trichobothrial numbers and trichobothrial patterns need to be carefully analyzed before being used to postulate taxonomic "affinities" among scorpion taxa. Stahnke's use of absolute trichobothrial numbers to characterize his subfamily Hadrurinae is unjustified. The fact that *Hadrurus* and *Anuroctonus* used to be included in the Vaejovinae before Stahnke's action is no reason to restrict comparisons to those genera assigned to it. As early as 1893 Pocock indicated that "no one will probably dispute that it [*Hadrurus*] is nearly allied to *Caraboctonus*."

CHELICERAL DENTITION. *Hadrurus, Hadruroides*, and *Caraboctonus* posses a well developed tooth on the inferior border of the movable finger of the chelicerae (Figs. 17, 18). Among all other non-buthid Recent scorpions this tooth is only found in *Iurus* and *Calchas* (Figs. 19, 20). *Anuroctonus* sometimes has a small denticle on this border (Fig. 21), but we do not consider it homologous to the large tooth mentioned above. Denticles on the inferior border of the movable finger of the chelicerae occur also in the Scorpiopsinae, and in *Paruroctonus* (Fig. 22), *Uroctonus*, and *Vaejovis* among the Vaejovinae. The condition observed in *Anuroctonus* is here hypothesized to be homologous to that of vaejovines, and that of *Hadrurus* to be homologous to *Hadruroides* and *Caraboctonus*.

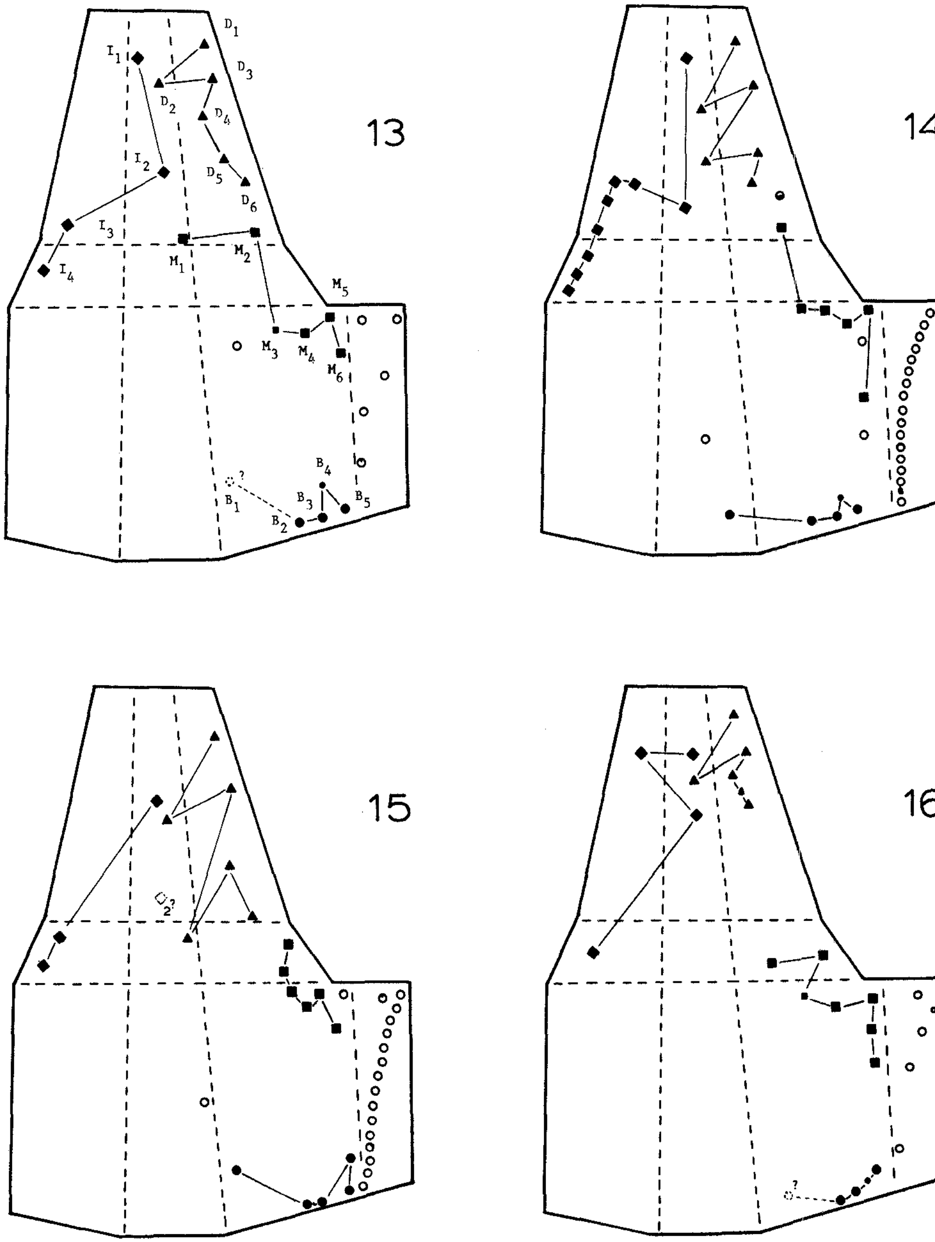
VENOM GLANDS. Pavlovsky (1924a) compared the morphology of venom glands in several scorpion genera, and recognized two basic types: Type I (Primitive) glands are unfolded, sac-like merocrine organs, and Type II (Complex) glands have one or more folds involving both the secretory epithelium and the basal membrane. Among the taxa we are concerned with, Pavlovsky reported Type I venom glands in *Uroctonus, Scorpiops,* and *Vaejovis*, and Type II venom glands in *Caraboctonus, Hadruroides, Hadrurus*, and *Iurus*.

Studies in progress on numerous scorpion taxa have confirmed Pavlovsky's findings and extended them. Among vaejovids Type I venom glands are present in *Anuroctonus,*



Figs. 9-12.–Diagrammatic illustrations of trichobothrial patterns of pedipalp chela showing homologies postulated by Vachon (1974): 9, *Hadruroides lunatus* (Koch); 10, *Hadrurus pinteri* Stahnke; 11, *Anuroctonus phaiodactylus* (Wood); 12, *Iurus dufoureius* (Brulle). KEY: ◆ = dorsal series of fixed finger, ▲ = external series of fixed finger, ● = Dorsal series of palm, ■ = External terminal series of palm, ○ = other trichobothria whose particular designations are not relavant here.

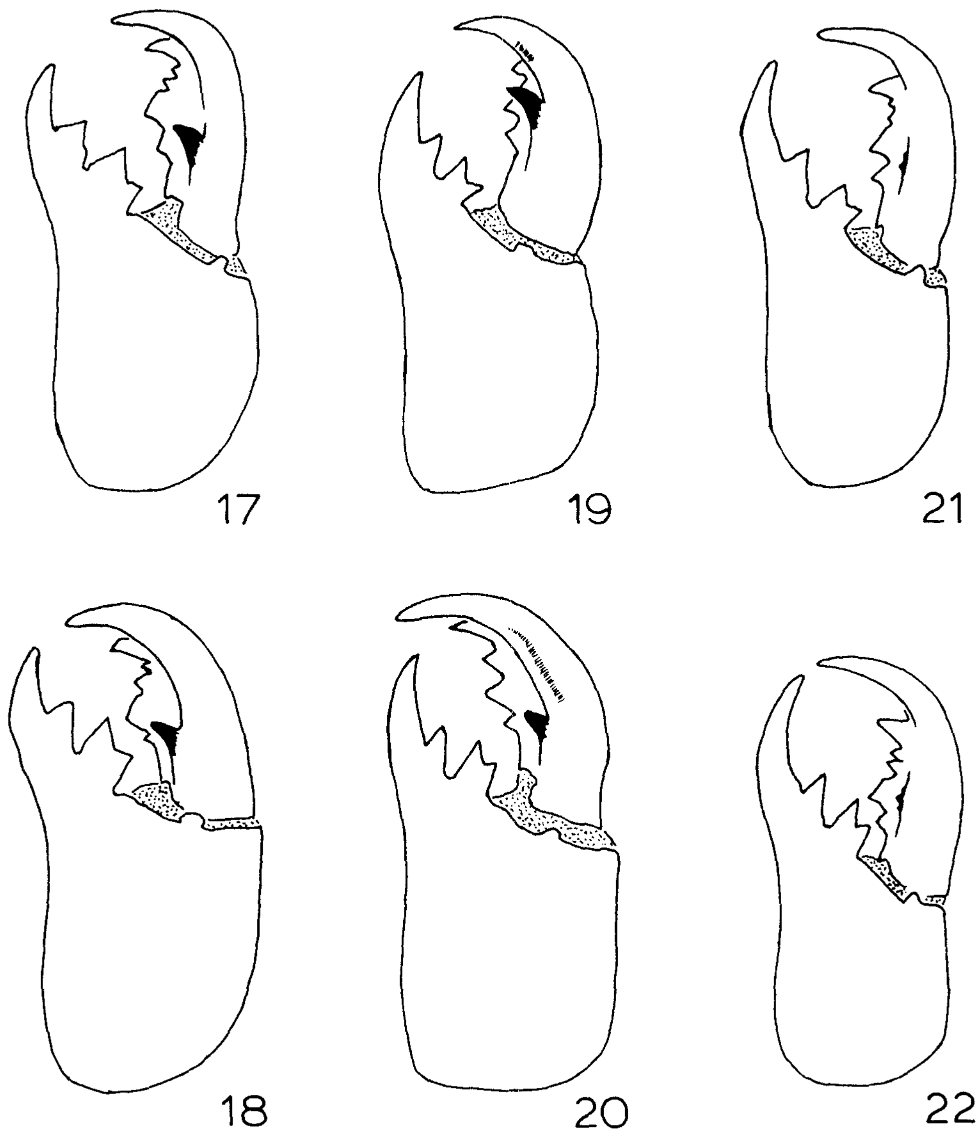
Paruroctonus, Paravaejovis Williams, *Serradigitus* Stahnke, and *Vejovoidus* Stahnke. Embryological studies (Pavlovsky 1924a, Probst 1972) have shown that folded glands are indeed derived from simple unfolded glands. Thus, we hypothesize that *Caraboctonus, Hadruroides*, and *Hadrurus* share a derived character state not found in *Anuroctonus*.



Figs. 13-16.–Diagrammatic illustrations of trichobothrial patterns of pedipalp chela showing homologies postulated by Stahnke (1974): 13, *Hadruroides lunatus* (Koch); 14, *Hadrurus pinteri* Stahnke; 15, *Anuroctonus phaiodactylus* (Wood); 16, *Iurus dufoureius* (Brulle). KEY: ♦ = Internal series of fixed finger, ▲ = Dorsal series of fixed finger, ■ = Median series of chela, ● = Basal series of palm, ○ = other trichobothria whose particular designations are not relevant here.

HEMISPERMATOPHORES. The spermatophore of *Hadrurus arizonensis* Ewing was recently described and noted to differ significantly from all described scorpion spermatophores (Francke 1979). Given the difficulties of obtaining scorpion spermatophores, several authors have opted to dissect and examine the hemispermatophores before they are deposited by males (e.g., Vachon 1952, Maury 1976, Koch 1977).

The hemispermatophores of *Hadrurus* (Figs. 23-26), *Hadruroides* (Figs. 27-33), and *Caraboctonus* (Figs. 34-37), are characterized by the absence of a capsule and the absence of a distinct truncal flexure. Their "triggering" mechanism, i.e., the action that enables



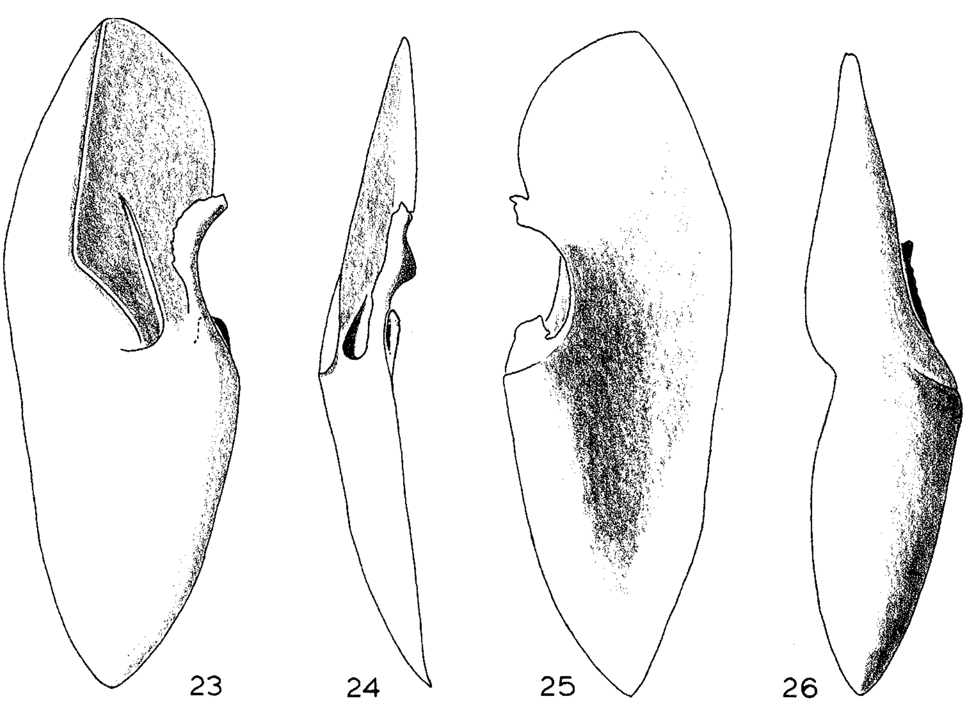
Figs. 17-22.—Ventral aspect of chelicera, showing dentition on both fixed and movable fingers. Note the conspicuous, large tooth (darkened) on the ventral aspect of the movable finger on figs. 17-20: 17, *Hadrurus arizonensis* Ewing; 18, *Caraboctonus keyserlingi* Pocock; 19, *Iurus dufoureius* (Brullé); 20, *Calchas nordmanni* Birula; 21, *Anuroctonus phaiodactylus* (Wood); 22, *Paruroctonus gracilior* (Hoffmann).

females to retrieve sperm (going from the preinsemination to the postinsemination state of the spermatophore), apparently resides in the broad flange that marks the mid-dorsal aspect of the hemispermatophore. [The genital operculi of the female separate and engage the flange on each side of the spermatophore.] The rounded, "free" lobes medial to the flange are presumably involved in the formation of the sperm duct which directs sperm from the trunk of the spermatophore into the genital opening of the female. A possible mechanism for sperm ejection in the absence of a truncal flexure has been proposed elsewhere (Francke 1979).

The hemisphermatophore of *Anuroctonus* (Figs. 38-41) has a well developed truncal flexure. A capsule, however, is apparently lacking, or if present consists of non-sclerotized membranes which could not be discerned by the techniques used in this study. Noteworthy are: the truncal flexure; the abrupt transition from trunk to lamella, marked by a pronounced inflection; and the small tooth mid-dorsally, which presumably engages the female genital operculum during sperm transfer.

The hemispermatophores of *Vaejovis* (Figs. 42-45), *Uroctonus* (Figs. 46-49), and *Paruroctonus* (Figs. 50-52), possess well developed truncal flexures and heavily sclerotized capsules. The abrupt transition from trunk to lamella with its pronounced inflection, and the mid-dorsal tooth, are similar (and perhaps homologous) to those in *Anuroctonus*.

Spermatophores and hemisphermatophores with well developed truncal flexures occur in bothriurids, scorpionids, diplocentrids, and some chactids in addition to the vaejovids cited above. A truncal flexure and a capsule are absent in buthid and chaerilid hemispermatophores, and their absence outside these groups is therefore considered plesimorphic

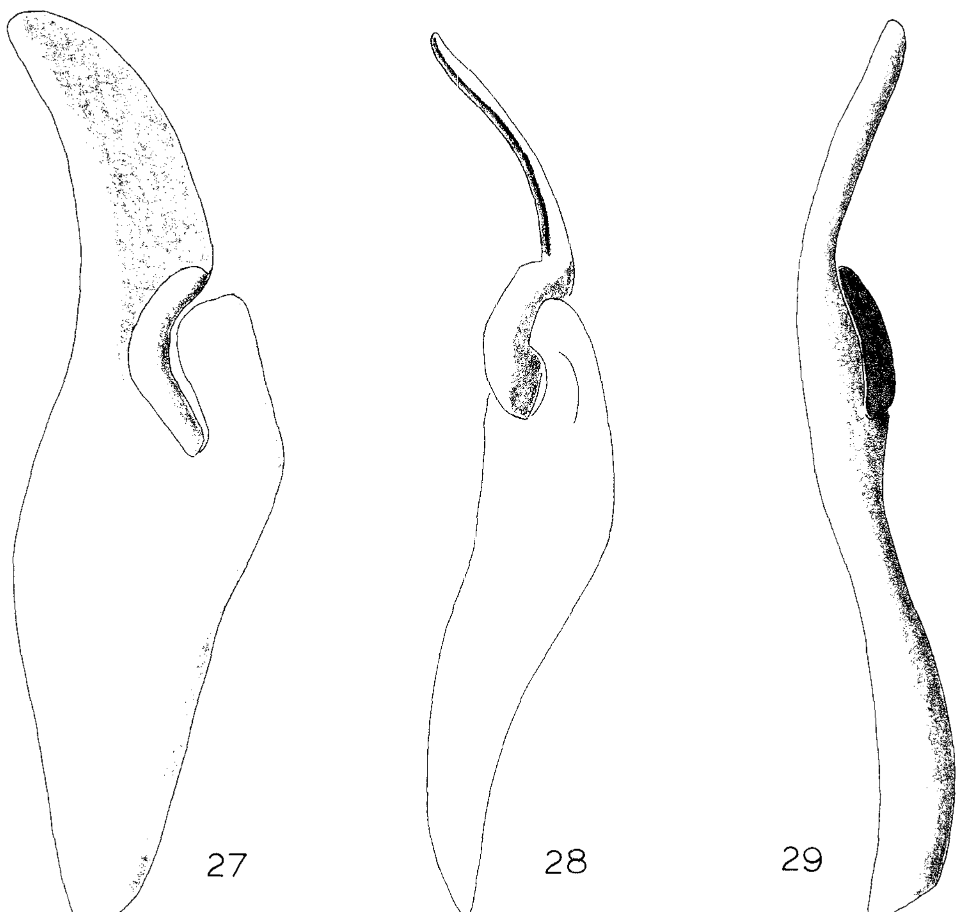


Figs. 23-26.–Hemispermatophore of *Hadrurus arizonensis* Ewing: 23, external aspect (dorsal region to the right); 24, dorsal aspect; 25, internal aspect; 26, ventral aspect. (Total length 10.0 mm)

(more general). The absence of a distinct truncal flexure and a capsule in the hemispermatophores of *Caraboctonus, Hadruroides*, and *Hadrurus* is therefore uninformative with respect to their phylogenetic relationships.

SPERMATOZOAN AXONEME. Jespersen and Hartwick (1973) studied the fine structure of spermiogenesis in some North American vaejovids. They found that the axonemal structure of sperm in *Hadrurus* is of a 9 + 1 pattern, whereas *Vaejovis, Uroctonus*, and *Anuroctonus* have a 9 + 0 pattern. They further indicate that a 9 + 2 pattern, as found in *Euscorpius* Thorell (Chactidae) is plesimorphic, and that the 9 + 1 and 9 + 0 patterns represent derived character states. Additional studies, especially of chactoids, are needed before phylogenetic hypotheses based on this character can be formulated. Nonetheless, this character fails to support Stahnke's hypothesized sister-group relationship between *Anuroctonus* and *Hadrurus*.

We have been unable to find any synapomorphies between *Anuroctonus* and *Hadrurus* that would corroborate the validity of Stahnke's subfamily Hadrurinae, and have found synapomorphies relating *Hadrurus* to *Caraboctonus* and *Hadruroides* instead. Whereas *Anuroctonus* appears to be more closely related to the Vaejovinae, where it was formerly placed, than either taxon is to *Hadrurus*, we are reluctant to place it back there on the

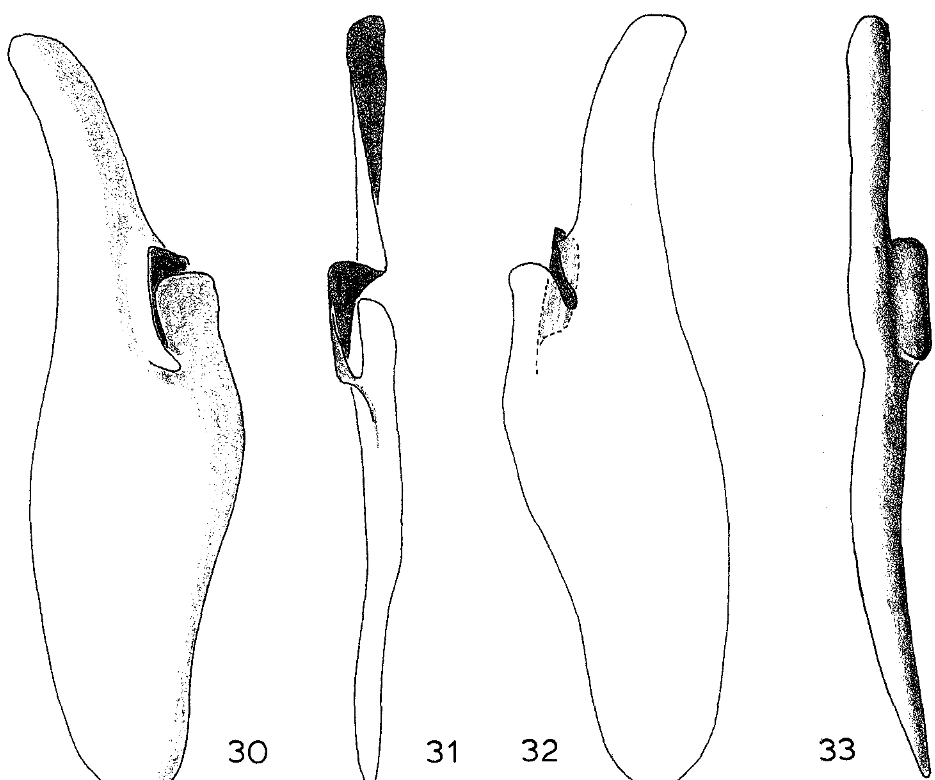


Figs. 27-29.–Hemispermatophore of *Hadruroides lunatus* (Koch): 27, external aspect (dorsal region to the right); 28, dorsal aspect; 29, ventral aspect. (Total length 3.5 mm)

basis of the hemispermatophore differences noted above. Further study is needed before the sister-group relationships of *Anuroctonus* can be hypothesized.

On the basis of cheliceral morphology, venom glands, and the trichobothrial pattern on the pedipalp chela fixed finger, we hypothesize that *Hadrurus* is more closely related to *Caraboctonus* plus *Hadruroides* than either taxon is to any other Recent scorpion.

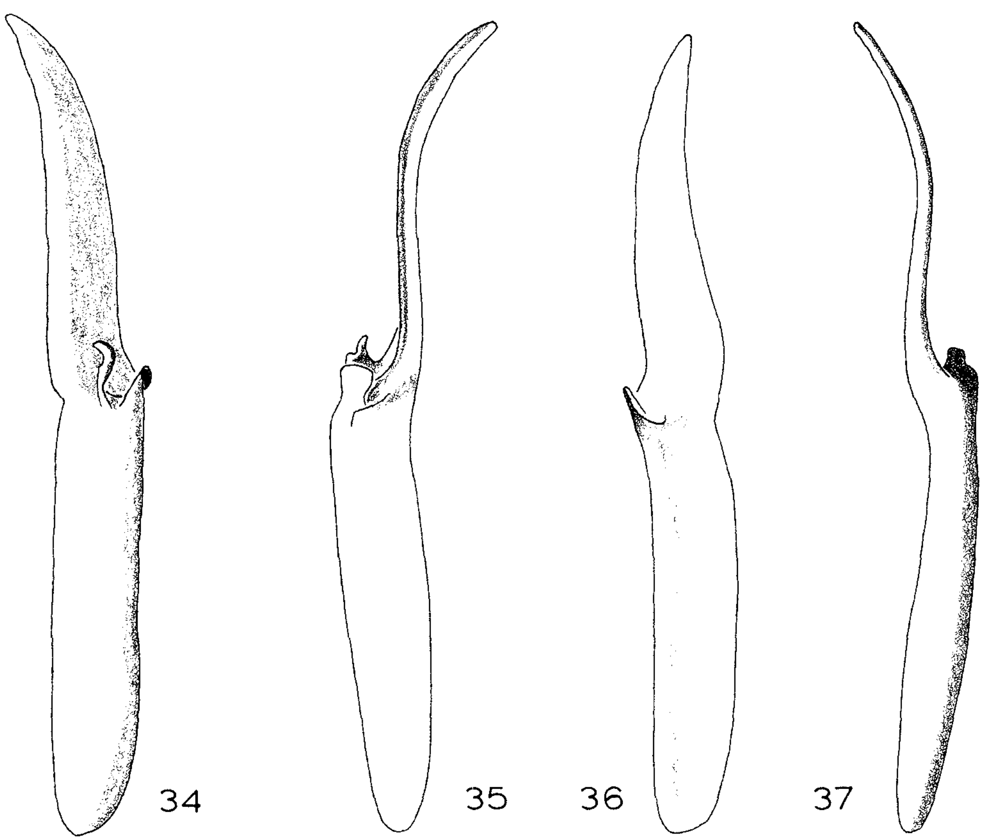
The relationships of *Calchas* and *Iurus*.–These two genera are presently placed each in a monogeneric subfamily in different families: *Calchas* Birula in the Calchinae (Chactidae), and *Iurus* Thorell in the Iurinae (Vaejovidae). The reason for these placements is obvious: *Calchas* reportedly has two pairs of lateral eyes, and *Iurus* has three pairs. Interestingly, however, Vachon (1966:456) diagnosed *Iurus* as follows: "... portant deux yeux latéraux (fig. 19), exceptionnellement trois d'un seul côte (fig. 20)"; yet his figures 19 and 20, based on the holotype of *Iurus dekanum* (Roewer) [= *I. dufoureius* (Brullé); Francke, in press] show ***four*** eyes on the left side and ***three*** on the right! The single specimen of *Calchas* we have studied [Turquie, Bilejdik, 23.IV.1971, MNHN-RS 6452, Max VACHON det.] clearly has three lateral eyes on the left side. These observations, coupled with the remarks made in the introduction about the unreliability of this character, invalidate the previous taxonomic assignments of these two genera. As indicated by Vachon (1971:718, quoted in the introduction), the trichobothrial patterns (Figs. 1-8), and the cheliceral dentition (Figs. 19, 20) of *Iurus* and *Calchas* are identical, and we might add unique among Recent scorpions. A clarification is in order regarding cheliceral dentition, for as stated earlier *Hadrurus, Hadruroides*, and *Caraboctonus* also have a



Figs. 30-33.–Hemispermatophore of *Hadruroides charcasus* (Karsch): 30, external aspect (dorsal region to the right); 31, dorsal aspect; 32, internal aspect; 33, ventral aspect. (Total length 4.0 mm)

prominent tooth on the inferior border of the movable finger of the chelicera: these three genera have two subdistal teeth on the dorsal border of the movable finger and have no serrula, while *Iurus* and *Calchas* have a single subdistal tooth dorsally and have a serrula (often quite worn down and difficult to see on adult *Iurus*, but prominent on immatures). The evidence is clear that *Iurus* and *Calchas* are more closely related to each other than either one is to any other Recent scorpion.

In the past *Calchas* has played a prominent role in discussions of scorpion phylogeny. Birula (1917) refers to it as the "missing link" between the Buthidae and Chactidae because it has tibial spurs on the third and fourth pairs of legs, as is typical of buthids, whereas other characters indicate chactid affinities. According to Vachon (1971) "Se dans leur ensemble, les Chactidae forment une transition entre Scorpionidae et Buthidae, les Calchinae soulignent avec nettéte les affinités entre Chactidae et Vaejovidae" [If Chactidae as a whole form a transition between Scorpionidae and Buthidae, Calchinae clearly underlines the affinities of Chactidae and Vaejovidae]. The fact that *Calchas* is the only non-buthid Recent scorpion with tibial spurs might lead some to question its hypothesized sister-group relationship with *Iurus*. However, since tibial spurs are widespread among buthids, and are also common on both fossil scorpions and eurypterids (Størmer 1963), their presence on *Calchas* seems plesiomorphic and uninformative at the level of generalization considered here.

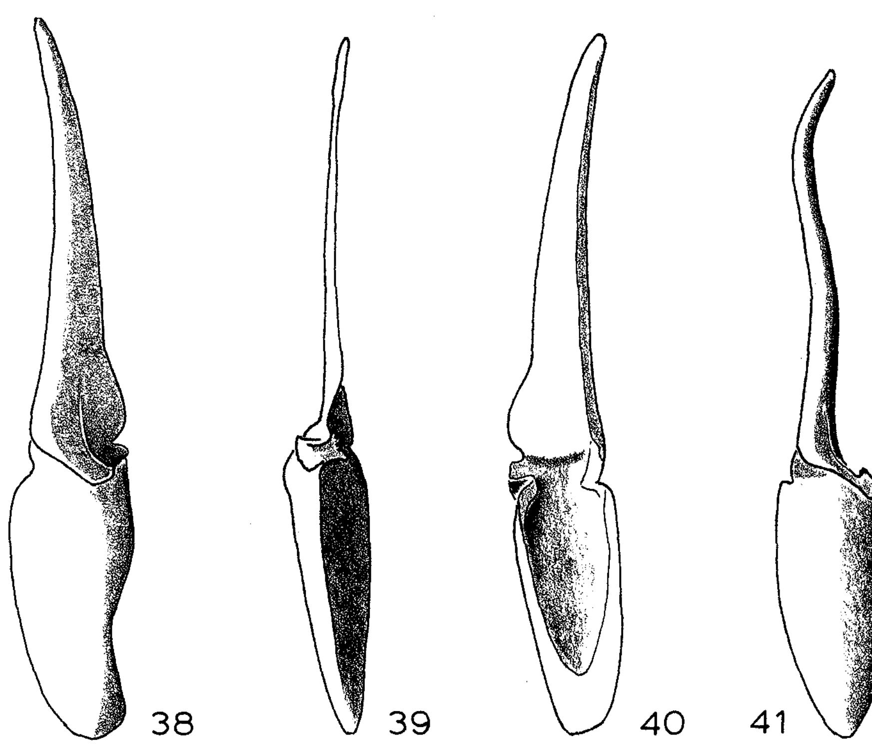


Figs. 34-37.—Hemispermatophore of *Caraboctonus keyserlingi* Pocock: 34, external aspect (dorsal region to the right); 35, dorsal aspect; 36, internal aspect; 37, ventral aspect. (Total length 6.8 mm)

The relationships of *Iurus* + *Calchas* to *Hadrurus* + *Hadruroides* + *Caraboctonus*.–As indicated by Pocock (1893, quoted as a preface here), *Iurus* and *Caraboctonus* share certain characters that "point to real kinship between the two." In light of previous sections, however, their relationships must be considered at a higher level of generalization: the taxon formed by *Iurus* + *Calchas* and the taxon formed by *Hadrurus* + *Hadruroides* + *Caraboctonus* with respect to all other Recent scorpions.

The two higher taxa in question share the presence on a prominent tooth on the inferior border of the movable finger of the chelicera. Outgroup comparisons with other members of the two families in which these five genera were formerly placed, as well as comparisons with all Recent scorpions indicate that this is a uniquely derived character shared by them. Thus, we hypothesize they are sister-groups.

Among chactoids *Caraboctonus, Hadruroides, Hadrurus,* and *Iurus* are the only known genera with complex venom glands. *Calchas* has simple venom glands. Two equally parsimonius hypotheses can be formulated to account for the difference between *Iurus* and *Calchas*. One hypothesis is that of character reversal in *Calchas*, i.e., the ancestor of *Iurus* + *Calchas* had complex venom glands, and after divergence *Calchas* reverted to simple glands (by neoteny ?). The second hypothesis is that of parallelism, i.e., *Iurus* and *Caraboctonus* + *Hadruroides* + *Hadrurus* independently acquired complex glands. Corroboration of the first hypothesis would lead to the conclusion that complex venom glands are a synapomorphy for the two higher taxa under consideration, whereas corroboration of the second hypothesis would refute the case for that synapomorphy. These alternative



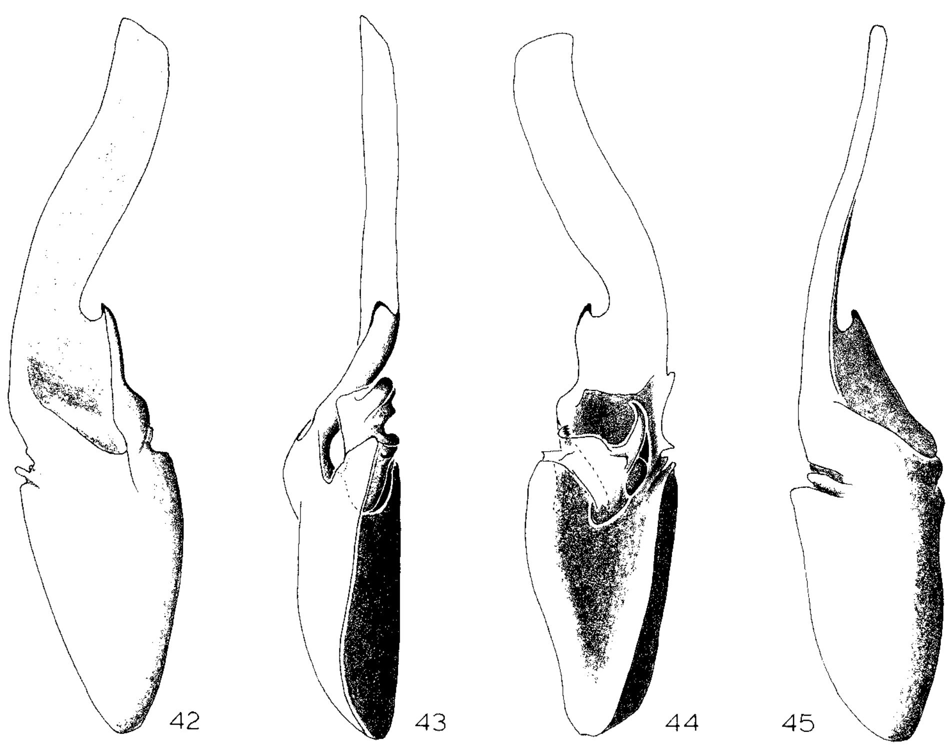
Figs. 38-41.–Hemispermatophore of *Anuroctonus phaiodactylus* (Wood): 38, external aspect (dorsal region to the right); 39, dorsal aspect; 40, internal aspect; 41, ventral aspect. (Total length 11.5 mm)

hypotheses can be tested by analysis of at least three transformation series (Platnick 1977), which are unavailable at this time.

The presence of a ventral median row of setaceous tufts in *Iurus* and *Caraboctonus* + *Hadruroides*, a character mentioned by Pocock (1893) as "the hairy clothing of the soles of the feet", appears to represent a parallelism (by parsimony). It would be most interesting, however, to examine first instar specimens of the genera in question because ontogenetic arguments might shed some light on the polarity of the transformation series (Nelson 1978), and the evidence could be used to expand the cladistic analyses presented here.

The hemispermatophore of *Iurus* (Figs. 53-56) has a distinct truncal flexure but lacks a capsule. Instead, a lightly sclerotized "lobe" develops along the terminal dilation of the vas deferens and the common duct that connects it with the seminal vesicle. Similar "lobes" occur in hemispermatophores of the Superstitioninae (Francke 1981) and may represent an early stage in the evolution of capsules in lamelliform spermatophores. The hemispermatophore of *Iurus* is similar in some respects to those of *Caraboctonus* (Figs. 34-37) and *Anuroctonus* (Figs. 38-41); most striking among these is the absence of a capsule, which as indicated earlier is plesimorphic and thus uninformative. The hemispermatophore of *Calchas* is unknown; Pavolvsky (1924b) illustrated the paraxial organs and these show that a truncal flexure is present as in *Iurus*.

We hereby hypothesize that *Calchas* + *Iurus* and *Caraboctonus* + *Hadruroides* + *Hadrurus* form a monophyletic group on the basis of the synapomorphy in their cheliceral morphology, i.e., the large tooth on the ventral edge of the movable finger. The



Figs. 42-45.–Hemispermatophore of *Vaejovis spinigerus* (Wood): 42, external aspect (dorsal region to the right); 43, dorsal aspect; 44, internal aspect; 45, ventral aspect. (Total length 7.0 mm)

taxonomic chaos prevalent among chactoids prevents us from carrying the cladistic analysis further at this time. The sister group of the monophyletic taxon proposed above remains unknown, and once it is recognized further characters will become available for analysis. Likewise, as more monophyletic groupings within the chactoids are identified, their relationships will be easier to reconstruct.

The phylogenetic relationships hypothesized in this section are diagrammatically illustrated by the cladogram in Fig. 57.

CLASSIFICATION AND TAXONOMY

The phylogenetic information contained in the cladogram (Fig. 57) is also expressed by the following sequenced classification:

- Family Iuridae Thorell, 1876, new rank
  - Subfamily Iurinae Thorell, 1876
    - *Iurus* Thorell, 1876
    - *Calchas* Birula, 1899
  - Subfamily Caraboctoninae Kraepelin, 1905
    - Tribe Caraboctonini, new
      - *Caraboctonus* Pocock, 1893
      - *Hadruroides* Pocock, 1893
    - Tribe Hadrurini, new
      - *Hadrurus* Thorell, 1876

The taxonomic changes resulting from this classification follow.

KEY TO SCORPION FAMILIES

1. Sternum subtriangular. Cheliceral movable finger with dorsal tine longer than ventral tine; with two basal teeth. Pedipalp femur with 10 or more trichobothria, of which 4-5 are on internal aspect. Pedipalp tibia without ventral trichobothria . . . . Buthidae

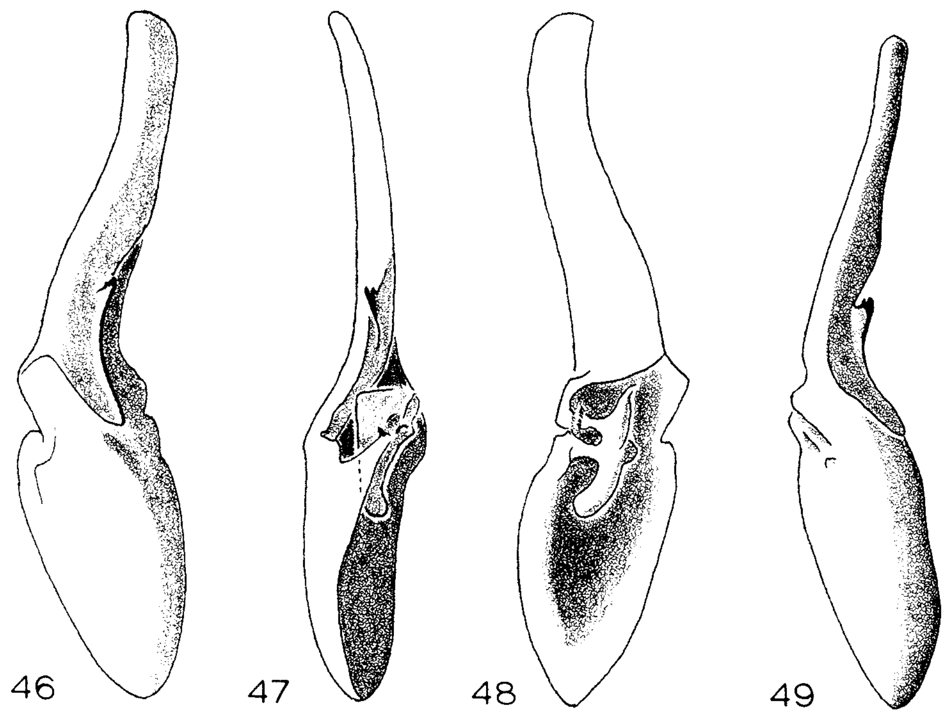
   Sternum not subtriangular, but pentagonal or slit-like. Cheliceral movable finger with dorsal tine shorter than ventral tine; with only one basal tooth. Pedipalp femur with 9 or fewer trichobothria, of which only one on internal aspect. Pedipalp tibia with one or more ventral trichobothria 2

2. Gnathocoxa broadly expanded anteriorly. Pedipalp femur with nine trichobothria, of which four are on dorsal aspect. Ventral trichobothria of tibia along ventrointernal keel . . . . Chaerilidae

   Gnathocoxa not broadly expanded anteriorly, but tapering gradually. Pedipalp femur with 3-4 trichobothria, of which only one on dorsal aspect. Ventral trichobothria of tibia along ventroexternal keel 3

3. Retrolateral pedal spurs absent. Female ovariuterus with conspicuous diverticula . . 4

   Retrolateral pedal spurs present. Female ovariuterus without diverticula 5



Figs. 46-49.–Hemispermatophore of *Uroctonus apacheanus* Gertsch and Soleglad: 46, external aspect (dorsal region to the right); 47, dorsal aspect; 48, internal aspect; 49, ventral aspect. (Total length 5.0 mm)

4. Subaculear tubercle present . . . . Diplocentridae

   Subaculear tubercle absent . . . . Scorpionidae

5. Sternum reduced to transverse, slit-like sclerite . . . . Bothriuridae

   Sternum not reduced to transverse, slit-like sclerite, but well developed and subpentagonal 6

6. Cheliceral movable finger with one well developed tooth on ventral margin. Venom glands complex, folded (except simple, unfolded in *Calchas*, which also has tibial spurs on legs III and IV) . . . . Iuridae

   Cheliceral movable finger without well developed tooth on ventral margin (several small denticles and/or tubercles may be present). Venom glands simple, unfolded . . . . "Chactoids" (Chactidae + Vaejovidae)

FAMILY IURIDAE THORELL

Type genus.–*Iurus* Thorell, 1876.

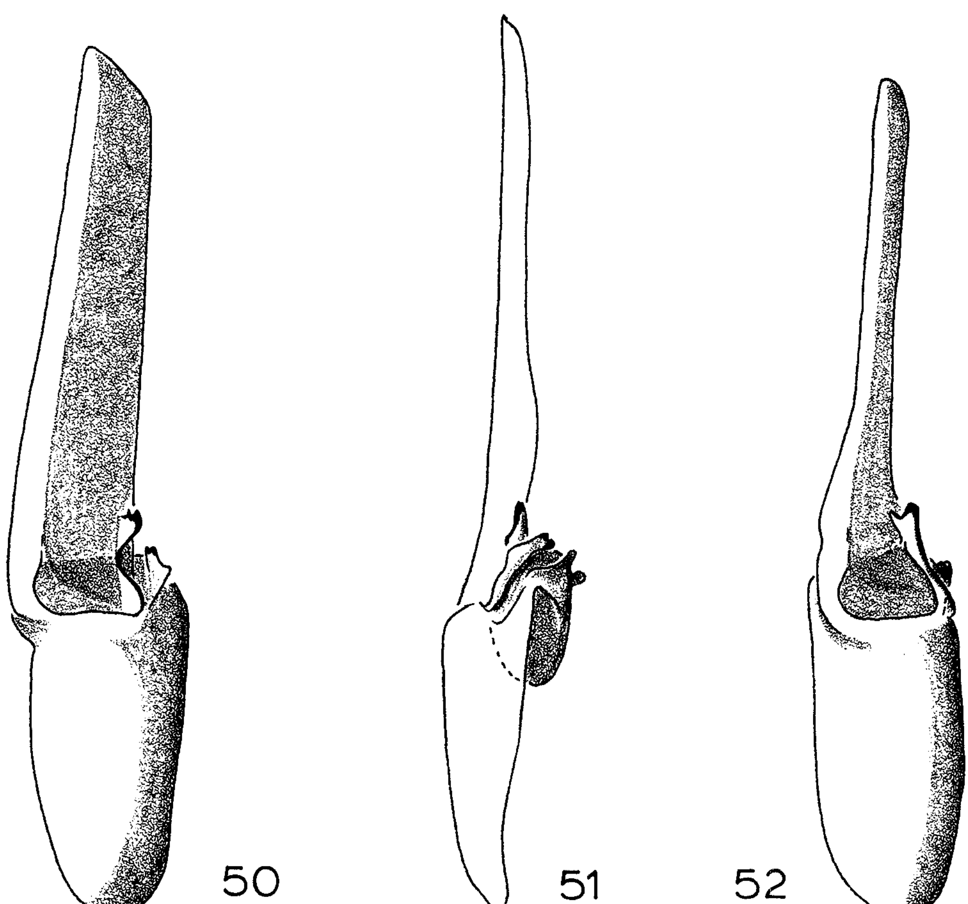
Included taxa.–Iurinae Thorell, 1876, and Caraboctoninae Kraepelin, 1905.

Diagnosis.–(1) Sternum pentagonal. Cheliceral movable finger (2) with dorsal distal tooth shorter than ventral distal tooth, and (3) with prominent ventral basal tooth. Pedipalp femur (4) with three trichobothria. Male reproductive system (5) without well developed, prominent accessory glands; (6) spermatophore lamelliform. Female ovariuterus (7) with four pairs of symmetrical transverse anastomoses, (8) lacking diverticula; (9) ova with little or no yolk. Venom glands (10) with several folds. Supraneural lymphatic gland (11) extends the length of the mesosoma, and two saclike lymphoid organs arise as diverticula of the diaphragm.

Comparisons.–The family Iuridae differs from the Buthidae in characters 1, 2, 3, 4, 5, 6, 7, 8, 9, and 11 above. Differs from Chaerilidae in that the gnathocoxa of leg I are not expanded anteriorly, and in characters 3, 4, 9, and 10. The Scorpioniodea are easily separated by characters 3 and 8; the Bothriuridae by characters 1, 3, and 9; and the chactoids by characters 3 and 10.

Subfamily Iurinae Thorell

Type genus.–*Iurus* Thorell, 1876.



Figs. 50-52.–Hemispermatophore of *Paruroctonus utahensis* (Williams): 50, external aspect (dorsal region to the right); 51, dorsal aspect; 52, ventroexternal aspect; 52, ventroexternal aspect. (Total length 7.0 mm)

Included taxa.—*Iurus* Thorell (Aegean Sea islands, Turkey, Greece), *Calchas* Birula, 1899 (Turkey; Georgian S.S.R., Russia).

Diagnosis.—Cheliceral movable finger with (1) a single subdistal tooth dorsally, and (2) a serrula ventrally (Figs. 19, 20). Trichobothrial pattern (Figs. 1-8, 12, 16): (3) tibia with a single trichobothrium ventrally; (4) internal aspect of chela fixed finger with one trichobothrium on distal one-half.

Comparisons.—Differs from the Caraboctoninae in characters 1-4 above (see Key to subordinate taxa of Iuridae).

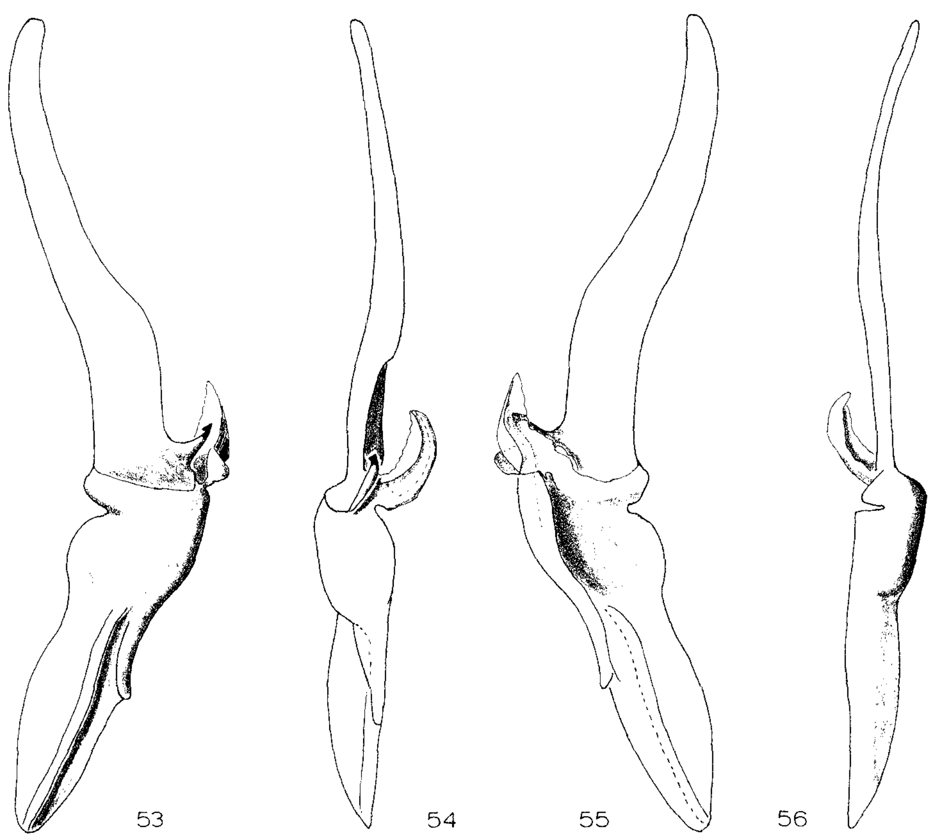
Remarks.—The two genera in this subfamily are easily separated by differences in pedipalp finger dentition, armature of the tibia of legs III and IV, setation on ventral aspect of tarsus, and shape of the stigmata (see Key to subordinate taxa).

Subfamily Caraboctoninae Kraepelin

Type genus.—*Caraboctonus* Pocock, 1893.

Included taxa.—Caraboctonini, new (western South America), Hadrurini, new (western North America).

Diagnosis.—Cheliceral movable finger with (1) two subdistal teeth dorsally, and (2) without serruly ventrally (Figs. 17, 18). Trichobothrial pattern (Figs. 9, 10, 13, 14): (3) tibia with two or more trichobothria ventrally; (4) internal aspect of chela fixed finger without trichobothria on distal one-half.



Figs. 53-56.—Hemispermatophore of *Iurus* sp.: 53, external aspect (dorsal region to the right); 54, dorsal aspect; 55, internal aspect; 56, ventral aspect. (Total length 14.0 mm)

Comparisons.–Differs from the Iurinae in characters 1-4 above (see Key to subordinate taxa of Iuridae).

Remarks.–The two tribes in this subfamily are easily separated by differences in pedipalp finger dentition, trichobothrial patterns, and setation on ventral aspect of tarsus (see Key to subordinate taxa). Additional differences include the hemispermatophores (Figs. 23-37), development of genital papillae on males, structure of pedal spurs, and development of unguicular claw (see respective diagnoses).

Tribe Caraboctonini, new

Type genus.–*Caraboctonus* Pocock, 1893.

Included taxa.–*Caraboctonus* Pocock (central Chile), *Hadruroides* Pocock, 1893 (Peru, Ecuador).

Diagnosis.–Pedipalp chela fingers with (1) 6-7 oblique rows of principal denticles. Trichobothrial pattern (Figs. 9, 13): tibia with (2) 15 trichobothria on external aspect, and (3) two on ventral aspect; palm of chela (4) without dorsal trichobothria, with (5) five trichobothria on ventral aspect. Legs with (6) pedal spurs simple; tarsus with (7) setaceous tufts ventrally, and (8) unguicular claw poorly developed. Males with (9) genital papillae well developed.

Comparisons.–Differs from Hadrurini in characters 1-9 above (see Key to subordinate taxa, and diagnosis of Hadrurini).

Remarks.–The two genera in this tribe can be separated by differences in pedipalp finger dentition, and shape of the sternum (see Key to subordinate taxa).

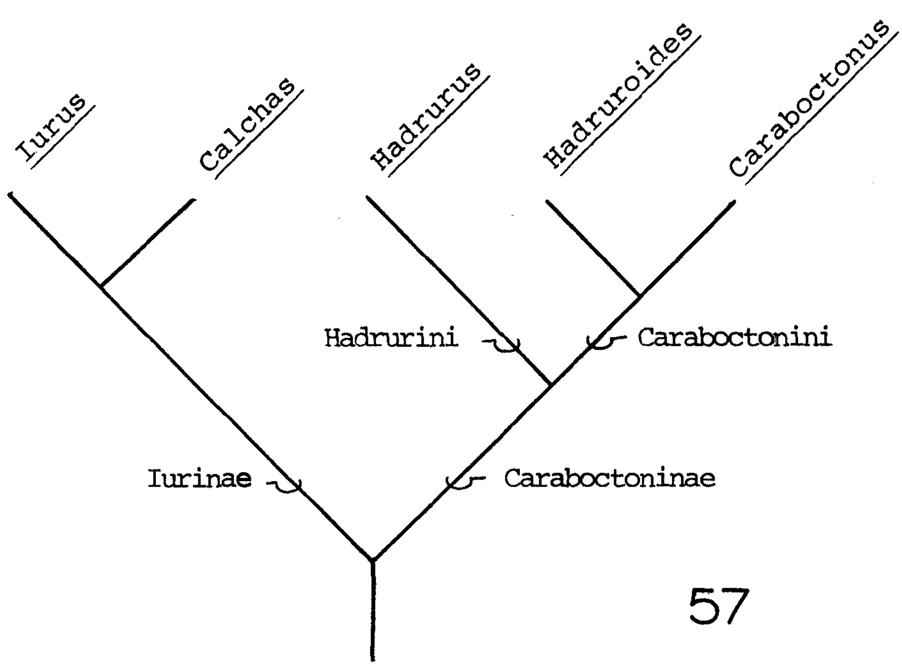


Fig. 57.–Cladogram illustrating the hypothesized phylogenetic relationships within the family Iuridae Thorell.

Tribe Hadrurini, new

Type genus.—*Hadrurus* Thorell, 1876. Monotypic.

Diagnosis.—Pedipalp finger with (1) 9-10 oblique rows of principal denticles. Trichobothrial pattern (Figs. 10, 14): tibia with (2) over 50 trichobothria on external aspect, and (3) over 30 on ventral aspect; palm of chela with (4) two dorsal trichobothria, and (5) over 12 on ventral aspect. Legs with (6) pedal spurs pectinate; tarsus (7) without setaceous tufts ventrally, and with (8) unguicular claw strongly developed. Males (9) without genital papillae.

Comparisons.—Differs from the Caraboctonini in characters 1-9 above (see Key to subordinate taxa, and diagnosis of Caraboctonini).

KEY TO SUBORDINATE TAXA OF IURIDAE

1. Cheliceral movable finger with one subdistal tooth dorsally, with serrula ventrally; pedipalp tibia with only one trichobothrium on ventral aspect; pedipalp chela fixed finger with one trichobothrium on distal one-half of internal aspect . . . . Iurinae . . . 2

   Cheliceral movable finger with two subdistal teeth dorsally, without serrula; pedipalp tibia with more than one trichobothrium on ventral aspect; pedipalp chela fixed finger without trichobothria on distal one-half of internal aspect . . . . Caraboctoninae . . . 3

2. Pedipalp chela fingers with 6-7 oblique rows of principal denticles; tibial spurs present on third and fourth pairs of legs; tarsus with two submedian rows of setae ventrally, without median row of setaceous tufts; stigmata small, oval . . . . *Calchas*

   Pedipalp chela fingers with 14-15 oblique rows of principal denticles; tibial spurs absent; tarsus with two submedian rows of setae ventrally, and with median row of setaceous tufts; stigmata long, slit-like . . . . *Iurus*

3. Pedipalp chela fingers with 9-10 oblique rows of principal denticles; tarsus with two submedian rows of setae ventrally, and with median row of short spines; pedipalp tibia with more than two (over 30 usually) trichobothria on ventral aspect, chela with more than four (about 13 to 27) on ventral aspect . . . . Hadrurini . . . *Hadrurus*

   Pedipalp chela fingers with 6-7 oblique rows of principal denticles; tarsus with two submedian rows of setae ventrally, and with median row of setaceous tufts; pedipalp with only two trichobothria on ventral aspect, chela with four trichobothria on ventral aspect . . . . Caraboctonini . . . 4

4. Pedipalp chela fingers on adults and subadults with internal and external supernumerary granules flanking the oblique rows of principal denticles; sternum as long as wide, with a deep longitudinal furrow . . . . *Hadruroides*

   Pedipalp chela fingers on adults and subadults without internal and external supernumerary granules flanking the oblique rows of principal denticles; sternum wider than long, without a deep longitudinal furrow (at most with a deep pit posteriorly) . . . . *Caraboctonus*

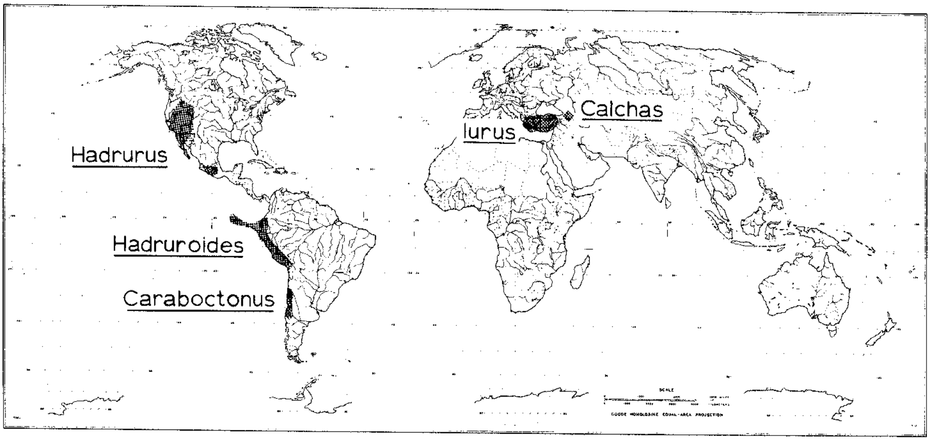


Fig. 58.–Geographical distribution of the five genera included in the family Iuridae Thorell.

ZOOGEOGRAPHY OF THE IURIDAE

The hypothesized phylogenetic relationships within the Iuridae are quite simple, as shown in the cladogram (Fig. 57). The basal dichotomy gives rise to the subfamilies Iurinae and Caraboctoninae: in the former a single subsequent dichotomy gives rise to the two genera of iurines; whereas on the latter the following dichotomy gives rise to the two tribes of caraboctonines, and a subsequent dichotomy in the Caraboctonini produced the two genera it contains. In addition, Soleglad (1976) recognized two species groups in *Hadrurus*: the *aztecus* group with two species in south-central Mexico (Oaxaca, Puebla, and Guerrero), and the *hirsutus* group with six species in Baja California and the southwestern United States. No futher subdivisions have been proposed for *Hadruroides*, the only other polytypic genus in the subfamily.

The geographical distribution of the family Iuridae might appear unusual to some, with *Calchas* in the Caucasus, *Iurus* with two species in the Aegean region (Francke, in press), *Hadrurus* in western North America, and *Hadruroides* and *Caraboctonus* in western South America (Fig. 58). This disjunct distribution nonetheless belongs to a biogeographic track, the "Tethys geosyncline," shared with many other organisms, among which the Malvaceae Malopeae, with allied genera in Chile, Peru, Mexico, the Mediterranean, Hungary and the Balkans, is a good example (Croizat 1958, chapter II).

The New World Caraboctoninae form part of the well known Southwestern Peru-Galapagos-Mexico track (Croizat 1958, chapter VIII). This track often involves the Revillagigedo Islands (off the Pacific coast of Mexico), from which only a *Vaejovis* sp. has been reported (Williams, 1980). The concepts of vicariance biogeography predict, however, the presence (now or in the past) of a caraboctonine on Revillagigedo, and it would be extremely interesting to collect more scorpions on those islands to test that prediction.

Geotectonic events possibly responsible for the vicariance patterns observed in iurids are first the opening of the North Atlantic during Jurassic times (Hallam 1971, Sclater and Tapscott 1979), isolating the two subfamilies on either side of that ocean. Secondly, the decoupling of the North American and South American plates, which formed a prominent role in the formation of the Caribbean region, during late Mesozoic to early Tertiary times (Rosen 1976), may have isolated *Hadrurus* in western North America and the Caraboctonini in western South America. By late Eocene to early Oligocene times, the Galapagos spreading center became active (Rosen 1976), leading eventually to the isolation of *Hadruroides maculatus galapagoensis* Maury on those islands. Likewise, the opening of the Gulf of California during the Pliocene (Moore and Buffington 1968) may have resulted in the split of the *aztecus* group of *Hadrurus* in south-central Mexico and the *hirsutus* group in Baja California and the southwestern United States. The break between *Iurus* and *Calchas* is probably related to tectonism involving the Turkish plate and the Anatolian fault sometime during the Tertiary. More precise dating should be possible as the geophysical history of that region becomes better known.

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