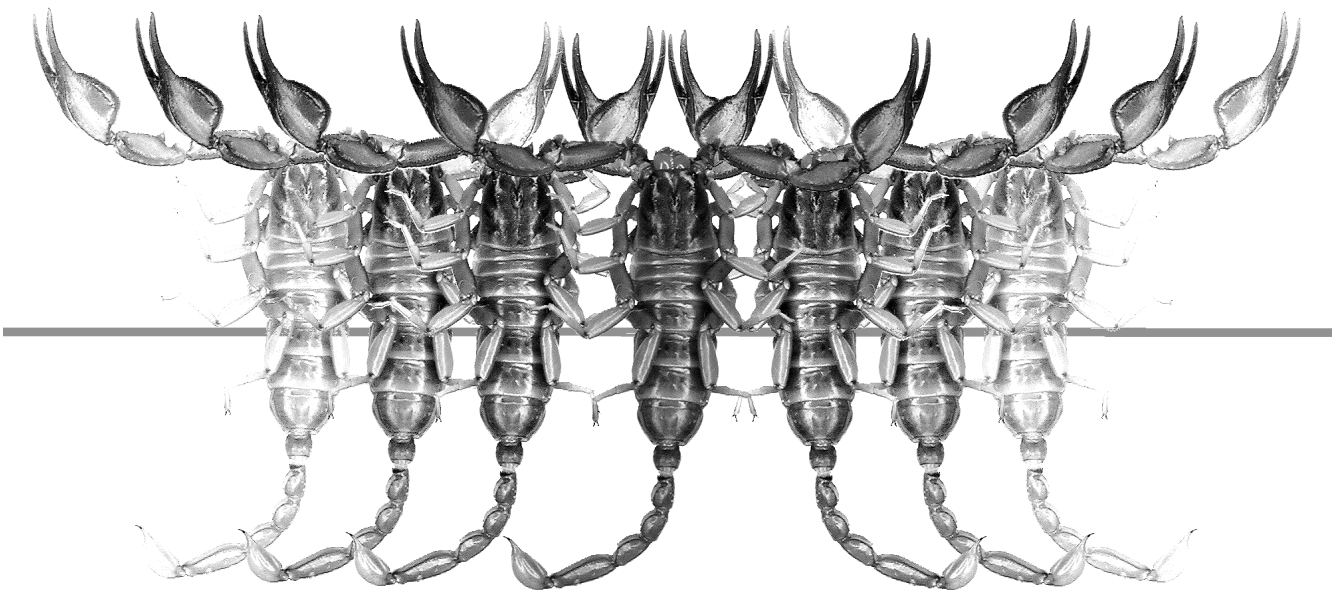


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**Evolution of Scorpion
Orthobothriotaxy —
A Cladistic Approach**

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Evolution of Scorpion Orthobothriotaxy: A Cladistic Approach

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Summary

This study presents a cladistic analysis of the derivation of orthobothriotaxic patterns in scorpions. Included in this analysis are the original three orthobothriotaxic patterns defined by Vachon (1972, 1974), the pattern of the unique scorpion *Pseudochactas ovchinnikovi* Gromov, 1998, and two trichobothrial patterns of fossil scorpions, the Upper Carboniferous palaeopisthacanthids and the Lower Cretaceous archaeobuthids. An overview of all fossil scorpion material where trichobothria are reported is presented in detail. The approach used in this analysis is to model the existence of an individual trichobothrium, adopting the 'absence of', 'petite size' and 'full size' as incremental stages of a trichobothrium's development. Of particular interest is the phylogenetic placement of *Pseudochactas* within Recent scorpions, for which the results of this study provide preliminary insight. Phylogenetic results of this analysis, based entirely on the derivation of orthobothriotaxic patterns, show that *Archaeobuthus* is the plesiomorphic sister group of all Recent scorpions, placed between the ancient palaeopisthacanthids and Recent scorpions. Within Recent scorpions, the clades 'buthids + pseudochactids' and 'chaerilids + Type C' are strongly endorsed by this analysis. Formal orthobothriotaxic types are defined for the palaeopisthacanthids (Type P), representing the earliest known complete fundamental trichobothrial pattern, and the pseudochactids (Type D), the fourth fundamental pattern for Recent scorpions.

Introduction

The goal of this study is to investigate the evolution of scorpion orthobothriotaxic patterns using cladistic techniques. Our secondary goal, in support of a companion paper (Soleglad & Fet, in progress), is to determine the phylogenetic placement of the recently described and unique scorpion *Pseudochactas ovchinnikovi* from Central Asia (Gromov, 1998). The satisfaction of these goals is further enhanced by two events: (1) the analysis of fossil scorpion trichobothria patterns conducted by Jeram (1994) and Lourenço (2001); and (2) the obtainment of actual specimens of *P. ovchinnikovi* for study. With Jeram and Lourenço's important contributions we are able for the first time to investigate the evolution of the basic trichobothrial patterns originally established by Vachon (1972, 1974) by incorporating fossil patterns. This effort is of particular interest since *Pseudochactas* itself represents another basic orthobothriotaxic pattern type for Recent scorpions (in addition to the three basic patterns defined by Vachon (1972, 1974)). In satisfaction of the second goal, the phylogeny of *Pseudochactas*, the trichobothria homologies established in this paper will become major characters that are combined with

other character analyses in the aforementioned companion paper. As stated by Gromov (1998, p. 1003) 'It is possible that the representative of this new family (Pseudochactidae) stands close to the common ancestor of all these families (the Recent scorpions)' --- *Pseudochactas* is certainly a basal member of Recent scorpions and, based on our current research, also shows significant affinity in some characters with the Carboniferous fossil scorpion family Palaeopisthacanthidae. Again, these comparisons are only made possible due to Jeram's (1994) comprehensive study of this group, Gromov's thorough description and excellent illustrations of *Pseudochactas*, and the availability of specimens of the latter.

Use of trichobothria in scorpion systematics

Max Vachon, in his monumental treatise on the formal presentation of scorpion trichobothrial patterns (Vachon, 1972, 1974), established the importance of trichobothria in upper level systematics by showing significant consistency across large numbers of genera in their basic patterns (i.e., orthobothriotaxy, as opposed to neobothriotaxy, a comparatively rare deviation from one of these

patterns). In this analysis, Vachon defined three fundamental orthobothriotaxic patterns that accounted for all recent scorpions. For example, the buthids, the largest scorpion aggregate, exhibited a pattern (Type A) not found in any other scorpion group. Similarly, a distinct pattern (Type B) was observed in all species of the genus *Chaerilus*, a taxon considered disjoint from all other scorpions and constituting a monotypic family Chaeriliidae. All other genera, spanning widely diverse groups conformed to a third pattern (Type C), a pattern considerably different from the other two. The significance of Vachon's three trichobothria patterns was quite appealing since they also reflected, in general terms, the current breakdown in upper-level scorpion systematics.

Sissom (1990) also considered these three fundamental patterns of key importance in scorpion systematics, illustrating the three patterns in detail as one of the important characters sets used in his overall diagnoses of Recent scorpion families. These illustrations were also accompanied by detailed trichobothria statistical data based on segment and surface (see Sissom, 1990, Table 3.1). Furthermore, Sissom (1990) also used trichobothrial patterns as his primary couplet in his extensive key to the buthid genera, segregating genera by the femoral *alpha* and *beta* patterns originally defined by Vachon (1975a). Fet & Rechkin (1990) presented the first quantitative (non-cladistic) analysis of all known variations in scorpion trichobothrial numbers, confirming three fundamental types of Vachon and separating several trends in trichobothrial variation.

To date three large-scale computerized cladistic analyses of scorpion systematics have been conducted, all using trichobothria as one of the primary character sets: (1) Stockwell (1989), in his unpublished Ph.D. thesis covering the entire order, defined 137 single-state characters, 42 of which dealt with trichobothria; (2) Prendini (2000) in his comprehensive treatment of the superfamily Scorpionioidea, defined 114 characters, single as well as multistate (a total of 147 character state derivations), of which 24 (36 state derivations) considered trichobothria; and (3) recently, Soleglad and Sissom (2001) in their revision of the family Euscorpiidae, defined 89 characters, single as well as multistate (a total of 154 state derivations), of which 31 (49 state derivations) involved trichobothria. It is clear from these three recent studies in scorpion phylogenetics that trichobothria are a primary character set since for all defined character state derivations, 25 – 32% dealt with trichobothria.

We believe that the trichobothrial systems found in scorpions are fundamental and basic to scorpion phylogeny. To further emphasize this point, we will show in this paper that their beginnings are found quite early in scorpion evolution.

Trichobothria Homology

In order to conduct a meaningful cladistic analysis, character homologies must be carefully established across all taxa involved in the analysis. This aspect of cladistics is by far the most important and also the most difficult since final results are totally dependent on these established homologies. In this section, we present the 'existence' approach to trichobothria evolution, an approach that directly addresses individual trichobothria. We present in detail proposed homologies across all fundamental orthobothriotaxic pattern types for each pedipalp segment --- the chela, patella and femur. In those situations where we established designations different from those of the original authors, we exercised the appropriate cladistic sequences to determine whether the alternative designations were consistent with overall parsimony (i.e., if any alternative designation increased the number of steps, it was excluded from consideration). In order to take advantage of the important trichobothria information now available on fossil scorpions (e.g., Jeram, 1994, Lourenço, 2001) we provide a detailed overview of our current knowledge of all reported trichobothria in fossil scorpions. This data will be used in establishing homologies for scorpion families Palaeopisthacanthidae and Archaeobuthidae, two components of our ingroup.

Trichobothria evolution modeling: an 'existence' approach

It has been widely accepted that the buthids (represented by trichobothrial pattern Type A) and the chaerilids (Type B) are the most primitive Recent scorpions (Lamoral, 1980; Stockwell, 1989; Sissom, 1990; Prendini, 2000; Soleglad & Sissom, 2001). If one accepts this presumed primitiveness, we can *grossly* ascertain the direction of trichobothria evolution on a segment by segment basis using the number of trichobothria. For the pedipalp femur, the numbers are higher compared to the presumed more recent taxa represented by Type C (i.e., 11 and 9 for Types A and B respectively, as compared to 3 for Type C) --- a 'many is primitive' hypothesis. In contrast, the patella has 13 trichobothria for Type A and 14 for Type B, as compared to 19 for Type C; i.e., a 'few is primitive' hypothesis. Similarly, the chela has 14 trichobothria for Type B and 15 for Type A, as compared to 26 found in Type C, again, a 'few is primitive' hypothesis.

Pseudochactas fits into these two 'number-based' hypotheses exhibiting counts of 12 trichobothria for the femur, which is the highest for all patterns, thus the most primitive if we accept the 'many is primitive' hypothesis; 10 for the patella, the lowest for all patterns, thus the most primitive if we accept the 'few is primitive' hy-

pothesis, and finally, 12 for the chela, again the lowest for all patterns and again the most primitive. Therefore *Pseudochactas* exhibits the most primitive condition for each segment based on gross trichobothria counts.

Our approach to trichobothria analysis is to model the various fundamental trichobothrial systems as proposed by Vachon (1972, 1974), Gromov (1998), Jeram (1994) and Lourenço (2001) by establishing consistent homologies across all the patterns and using cladistic analysis to evaluate these hypothesized homologies — which means accepting homologies that are the most efficient with respect to trichobothrium gains or losses (i.e., the most parsimonious). This approach is more comprehensive than the gross ‘number approach’ discussed above since individual trichobothrium derivation is considered. We model the ‘existence’ of individual trichobothria by using a Sankoff character approach (‘stepmatrix’ in PAUP* (Swofford, 1998)) to the absence or presence of a trichobothrium. We consider three states for a trichobothrium’s existence: (1) absent, (2) ‘petite’ in size, and (3) full size. We suggest here that a petite trichobothrium is a trichobothrium that is either evolving to a full trichobothrium or, is in the process of being lost. We assign a cost (i.e., a cladistic ‘weight’) of ‘one’ for the state transitions of ‘absent ↔ petite’ or ‘petite ↔ full’ and a cost of ‘two’ for the transition ‘absent ↔ full’, therefore modeling the intermediate state of a petite trichobothrium. It is clear using this approach that the number of steps isolated for most parsimonious topologies is based on the individual homologies established. If suggested homologies imply considerable gains and losses of individual trichobothria, the resulting topologies will not be parsimonious. See **Appendix A** for a detailed overview of petite trichobothria in Recent scorpions and examples supporting the assumption of petite trichobothria as an intermediate state of development. **Appendix C** contains details of the Sankoff character definition as well as individual taxon/character state mappings for the three segments of the pedipalp. Note that using an ordered multistate character in lieu of Sankoff will give the same results as long as the state weight changes are incremental by one. However, for compatibility with other studies in progress, we use Sankoff which is not restricted to constant weight increments across state changes.

Trichobothria reported in the fossil record

Kjellesvig-Waering (1986) redescribed and illustrated in detail the palaeopisthacanthid *Palaeopisthacanthus schucherti* Petrunkevitch, including suggested trichobothria patterns of the pedipalp (Text-Fig. 104). This was the first mention of trichobothria for fossil scorpions dating back to the Upper Carboniferous period. Stockwell, for the femur and patella (1989, pp. 98-100), and

Prendini, for the patella (2000, p. 55), used Kjellesvig-Waering’s trichobothria data as a basis for some polarity argumentation for trichobothria-based characters. Jeram (1994) reevaluated all Carboniferous palaeopisthacanthid fossil data including new material, and provided considerably more information on the trichobothria patterns originally discussed by Kjellesvig-Waering. Recently, Lourenço & Weitschat (1996, 2000), Lourenço (2001) and Carvalho & Lourenço (2001) described important fossil material from sources dating back to the Cretaceous and Tertiary (Eocene) periods. New World fossils have been described and/or discussed by Schawaller (1979, 1981), Santiago-Blay & Poinar (1988, 1993) and Santiago-Blay *et al.* (1990) from both Dominican and Mexican amber, spanning Miocene to Eocene epochs. Presently, new Cretaceous material from the Santana Formation in Brazil is being evaluated (Santiago-Blay *et al.*, 2001). In all of these recent developments trichobothrial patterns are discussed or described, some having more relevance to this present study than others.

Of all these fossil data, we consider two patterns complete enough to incorporate into our cladistic analysis: the palaeopisthacanthids (Jeram, 1994), based on several species and the archaeobuthids, based on a single but quite visible specimen from the Cretaceous amber (Lourenço, 2001).

Palaeopisthacanthids: In 1994, Andrew Jeram reviewed the phylogeny of Upper Carboniferous scorpions (323-290 Ma) which included a complete reevaluation of the palaeopisthacanthids. Within the Palaeopisthacanthidae, Jeram (1994) defined one new genus and two new species. Although this important work also contains significant new morphological analysis involving chelal finger dentition, cheliceral armature, metasomal carination, etc, all of which are directly relevant to the phylogenetic analysis of Recent scorpions, the detailed trichobothria analysis presented is of particular interest to our current effort. The remarkable detailed analysis provided by Jeram is indeed impressive: although trichobothria were identified in almost all cases by the enlarged ‘cup-shaped’ follicle, Jeram was able, in one case, to actually isolate a trichobothrium bristle (p. 529)!

As discussed and described in Jeram (1994) as well as reported in the *Catalog of Scorpions of the World* (Fet, 2000a) the family Palaeopisthacanthidae is composed of three genera comprising four species: *Palaeopisthacanthus schucherti* Petrunkevitch, *P. vogelandurdeni* Jeram, *Composcorpius elegans* Petrunkevitch and *Cryptoscorpius americanus* Jeram. Also of interest to the present study is the taxon *Corniops mapezii* Jeram, which is tentatively placed in the Orthosterni (*incertae sedis*) but whose family placement is undetermined. This interesting taxon appears to be a prototypic palaeopisthacanthid, exhibiting important differences from the family. In particular, the trichobothria follicles are smaller and simpler

lacking the rimmed ‘cup-like’ shape found in the palaeopisthacanthids and all Recent scorpions. We suggest here that this taxon may be representative of some of the earliest scorpion trichobothrial patterns to date. Jeram (Text-Fig. 1) placed *Corniops* basal to the palaeopisthacanthids based both on these simplistic smaller trichobothria and the straight chelal finger denticle row (in the palaeopisthacanthids this row is broken up into slightly oblique subgroups).

Table 1 presents all trichobothria reported by Jeram for the four palaeopisthacanthids and *Corniops mapesii*. It is clear from the data in this table, as well as from a close look at the descriptions provided by Jeram, that the trichobothrial data are probably incomplete on some of the pedipalp segment surfaces. On most of the fragmentary segment data available to Jeram it is clear that not all surfaces were visible for examination. Also of interest, is that Jeram proposed different trichobothrial patterns and numbers for *Palaeopisthacanthus* and *Compsoscorpium*, even though the data appears to be incomplete. Based on the frugality of basic patterns found in Recent scorpions spanning over 1600 species and subspecies and 180 genera and subgenera (Fet *et al.*, 2000), it seems unlikely that we would have two basic pattern types occurring within the palaeopisthacanthids based on only four species. Therefore, we have taken the liberty of defining a ‘composite’ palaeopisthacanthid trichobothrial pattern based on the following set of rules: (1) we accept Jeram’s observation when he identifies a trichobothrium; and (2) we create a composite pattern per surface based on all four species using *logical union*. As can be seen in Table 1, the hypothesized chelal pattern (11 trichobothria) is the same as that reported by Jeram for species *P. schucherti*, therefore we do not need to construct a composite for this segment. We consider the chela pattern as reported by Jeram to be the most complete Carboniferous fossil pedipalp segment available to date. However, the patella (three trichobothria) is a composite of *P. schucherti* and *Compsoscorpium elegans*, and the femur (four trichobothria) a composite of *P. schucherti* and *Cryptoscorpium americanus* and possibly *C. elegans* (see Fig. 1 for the composition of the femur and patella patterns based on logical union). As evident from Table 1, out of the entire set of 18 proposed pedipalp trichobothria, 13 are supported by at least two species and in some cases by three or four.

We did find it interesting that Jeram (1994) did not report any internal trichobothria for the entire pedipalp. Although internal trichobothria comprise the second lowest number of trichobothria for the four basic surfaces of Recent scorpions (i.e., 22 internal and 14 ventral versus 39 dorsal and 83 external --- sums taken across the four types), we suspect that internal trichobothria could have existed to some degree in the palaeopisthacanthids, especially for the femur (which has the highest total number of internal trichobothria for all four Recent

scorpion orthobothriotaxic types). Studying Jeram’s paper, only the internal surface of the chela of *P. schucherti* and *C. americanus* were available for examination (at least these were illustrated in part). Therefore, it appears that the internal surface of the femur was not readily visible in the material examined by Jeram.

Archaeobuthids: Recently, Wilson Lourenço (2001) described a remarkable fossil scorpion from the amber of Lebanon, *Archaeobuthus estephani*, dating back to the Lower Cretaceous period (125 Ma). Of particular importance to this study is that, evidently, all trichobothria are visible, this from a specimen only 6 mm. in length. Table 2 depicts the trichobothria identified by Lourenço with a few of the designations changed based on homology analysis discussed elsewhere in this paper. In Table 2 the trichobothria of *Archaeobuthus* are contrasted with the standard Type A pattern found in the buthids. It is evident from Table 2 that this fossil taxon is lacking several trichobothria found in Type A (13 out of 39 trichobothria). For the chela, trichobothria *it*, *Eb₃*, *Et₄* (our designation for *Esb*) and *V₂* are absent; for the patella, five trichobothria are absent, *d₃*, *d₄*, *et₂*, *esb₁* and *eb₂*; and for the femur, four trichobothria are missing, *i₃*, *i₄*, *e₁* and *e₂*. Note that for the femur we have decided, based on comparison with other fossil material, that the solitary external trichobothrium reported should be designated as *e₃*, a trichobothrium not found in the standard Type A pattern. The data presented in Table 2 is derived both from Lourenço’s Figs. 10-11 & 13-14 and text that individually lists the trichobothria (p. 646).

Interestingly, Lourenço considers *Archaeobuthus* (for which he also creates the family Archaeobuthidae) a member of the superfamily Buthoidea. One of the reasons Lourenço gives is the lack of ventral trichobothria on the patella, which is characteristic of the buthids and microcharmids (Lourenço, 2001, p. 646). However, *Pseudochactas* also shares this character of absent patellar ventral trichobothria, a taxon Lourenço recently combined with the chaerilids which have ventral trichobothria on the patella (Lourenço, 2000). Lourenço also discusses the femoral *alpha-beta* affinity of *Archaeobuthus*: trichobothria *d₁*, *d₃* and *d₄* are essentially linear, thus was not assignable to a type. However, Lourenço does state that the trichobothria patterns exhibited in *Archaeobuthus* do ‘place the new family in an isolated position in relation to both the Microcharmidae and the Buthidae.’ We certainly agree with this observation, since *Archaeobuthus* is missing no less than one-third of the trichobothria designated for Type A scorpions (i.e., the buthids and microcharmids). Elsewhere in this paper we investigate in detail the taxonomic place of *Archaeobuthus* using trichobothrial patterns.

Brazil - Santana Formation: Campos (1986) was first to describe a fossil scorpion from the Santana formation in Brazil (Lower Cretaceous; 110 ± 10 Ma) named *Araripescorpium ligabuei* (familial placement was not

| | Femur (4) | | | Patella (3) | | | Chela (11) | | | | | | | | | | | |
|---------------------------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|------------------------|------------------------|-----------|------------|-----------|------------------------|------------|------------------------|------------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| | <i>d</i> ₁ | <i>d</i> ₃ | <i>d</i> ₅ | <i>e</i> ₃ | <i>d</i> ₁ | <i>eb</i> ₁ | <i>et</i> ₁ | <i>eb</i> | <i>est</i> | <i>et</i> | <i>Et</i> ₁ | <i>Est</i> | <i>Eb</i> ₁ | <i>Eb</i> ₂ | <i>V</i> ₁ | <i>V</i> ₂ | <i>V</i> ₃ | <i>V</i> ₄ |
| <i>Palaeopisthacanthus schucherti</i> | X | - | - | X | X | - | X | X | X | X | X | X | X | X | X | X | X | X |
| <i>P. vogelandurdeni</i> | - | - | - | - | - | - | - | X | - | - | X | - | - | - | - | - | - | - |
| <i>Composcorpheus elegans</i> | 1 | 1 | 1 | 1 | - | X | X | X | X | X | 2 | 2 | 2 | 2 | X | X | 2 | 2 |
| <i>Cryptoscorpheus americanus</i> | X | X | X | - | - | - | - | X | X | - | X | - | - | - | X | X | X | X |
| <i>Corniops mapesii</i> ³ | - | - | - | - | - | - | - | X | - | - | - | X? | - | - | X | X | - | - |

Table 1: Trichobothria reported for the palaeopisthacanthids and other orthosterni (after Jeram, 1994). X = reported and/or illustrated. ¹ three trichobothria reported but not individually identified. ² eight trichobothria reported, six illustrated. ³ Trichobothria originating from enlarged follicles, but not cup-like as present in the palaeopisthacanthids and all Recent scorpions. Note that individual trichobothrium designations are based on the analysis presented in this paper and, therefore, do not necessarily reflect those designations as originally established by Jeram.

| | Femur (11) | | | | | Patella (13) | | | | | Chela (15) | | | | | | | | | | |
|----------------------------|------------|----------|----------|----------|----------|--------------|----------|----------|----------|----------|------------|----------|----------|----------|----------|----------|----------|----------|----------|----------|---|
| | <i>i</i> | <i>d</i> | <i>e</i> | <i>1</i> | <i>2</i> | <i>3</i> | <i>4</i> | <i>5</i> | <i>i</i> | <i>d</i> | <i>e</i> | <i>1</i> | <i>2</i> | <i>3</i> | <i>4</i> | <i>5</i> | <i>i</i> | <i>d</i> | <i>e</i> | <i>v</i> | |
| <i>Palaeolychas</i> | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| <i>Palaeoprotobuthus</i> | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| <i>Palaeotityobuthus</i> | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| <i>Palaeoakentrobuthus</i> | X | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Palaeo-Composite | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| <i>Archaeobuthus</i> | X | X | - | - | - | - | - | X | X | X | X | X | X | X | X | X | X | X | X | X | X |

Table 2: Partial trichobothria patterns reported for four Eocene ‘palaeo-buthid’ genera (Lourenço & Weitschat, 1996, 2000) and complete pattern for Cretaceous *Archaeobuthus* (Lourenço, 2001) contrasted with standard Type A designations. ‘Palaeo-composite’ is a composite of all four ‘palaeo-buthid’ genera. * *e*₃ is reported for *Archaeobuthus* only, not occurring in standard Type A pattern.

made). In the brief diagnosis, trichobothria were not reported for this species therefore, per se, it is not of particular interest to this current study. However, the overall morphometrics of the body and gross shape of the pedipalp are very similar to that exhibited on the other two Santana specimens discussed below. In comparison to Recent scorpions found in South America, the overall body and pedipalp shape of *Araripescorpius* are similar to that found in some bothriurids, in particular *Bothriurus*, the chactids (e.g., *Brotheas*), and the ischnurids (e.g., *Opisthacanthus*), definitely excluding the buthids.

Carvalho & Lourenço (2001) recently described another important fossil scorpion from the same Santana formation. The importance of this specimen, *Protoischnurus axelrodorum* (family Protoischnuridae), is that it clearly appears to be an archetypic representation of the Type C orthobothriotaxic pattern. Unfortunately, the trichobothrial pattern is not complete (in our opinion) and therefore cannot be included in the cladistic analysis conducted in this paper. The authors state 'Trichobothrial pattern of the 'basic' type C: probably neobothriotaxic minorante in the sense of Vachon'. Only ten trichobothria are reported: six for the chela, V_1 - V_4 , eb and Et_5 ; four for the patella, v_1 - v_2 , est and et ; and none for the femur. Although the authors suggest the specimen is 'probably neobothriotaxic minorante', which if taken literally, implies that these are all the trichobothria found on the specimen, we strongly believe that all trichobothria are not detectable, and thus not reported. Otherwise, this specimen would have considerably less trichobothria than that reported for the much older Carboniferous palaeopisthacanthids. In addition, to support this opinion, we are currently investigating another Santana fossil specimen which exhibits a different trichobothrial pattern (albeit, also only partial), see below. Characters which support Carvalho & Lourenço's ischnurid connection (in contrast to a chactid, for example) are the exaggerated patellar spur found on the pedipalp (Fig. 15) and the three lateral eyes per side (Fig. 8). In addition, for the chela, it is particularly interesting to note that the large space separating trichobothria V_2 and V_3 exhibited in many scorpionoids is also present in *Protoischnurus* (compare Vachon, 1974, Figs 119-124 of two Recent ischnurid genera to Carvalho & Lourenço, 2001, Fig. 14). The assigned designation of chelal trichobothria eb and Et_5 are probably in reference to those as seen in a typical ischnurid with eb being located on the distal aspect of the palm (see e.g. Vachon, 1974, Fig. 119). The presence of ventral trichobothria on the patella is probably the most significant character indicating a non-buthid species since they are only found in Type B and Type C patterns. Also, the four trichobothria found on the chelal ventral aspect are indicative of Type C, albeit they are also present in the ancient palaeopisthacanthids.

Currently, Santiago-Blay *et al.* (2001; in progress) are investigating another Santana formation fossil scorpion with overall body and pedipalp proportions similar to that seen in both *Araripescorpius* and *Protoischnurus*. Of interest to this present study, three trichobothria are visible on the dorsal-external aspect of the chelal fixed finger of this specimen (others could be uncovered as the investigation continues). The most plausible designation of these three trichobothria are db , dsb and dst , when compared to Recent scorpions. It is this specimen, in particular, that suggests that the pattern reported for *Protoischnurus* could be incomplete, since it is unlikely we would have two Early Cretaceous non-buthid fossil scorpions from the same formation that exhibit fundamentally different orthobothriotaxic patterns, both prototypical Type C. That is, we are suggesting here that both *Protoischnurus* and this new fossil specimen probably share the same overall trichobothrial pattern type, a prototypical Type C.

'**Palaeo-buthids**': Lourenço & Weitschat (1996, 2000) described four new fossil genera from Baltic amber, *Palaeolychas*, *Palaeotityobuthus*, *Palaeoprotobuthus* and *Palaeoakentrobuthus*. The deposit the amber is found in is from the Eocene, 55 Ma, but the amber itself may be 5-10 Ma older. From a trichobothria perspective, only partial patterns are available from each taxon described. In Table 2 we present all trichobothria identified by Lourenço & Weitschat including a composite of all four genera taken together. Based on the occurrence of many presumably important trichobothria we suspect that these four fossil genera probably did exhibit the standard Type A pattern attributed to the buthids and therefore the fossil genera are contrasted with the Type A configuration. In particular chelal trichobothria i , Eb_3 and V_2 , patellar d_3 , d_4 and eb_2 , and femoral i_3 , e_1 and e_2 imply that these 'palaeo-buthids' are consistent with Type A. All of these important trichobothria are *absent* in the Cretaceous *Archaeobuthus*, a species Lourenço (2001) hypothesized as a buthoid. As can be seen from the composite of these four genera, 31 trichobothria (out of 39 total for Type A) are actually identified. Since these four fossil buthid genera give us important information as to the 'time-line' of the Type A pattern, their importance will be discussed further in this paper.

'**Fossil New World buthids**': Schawaller (1979, 1981) named two new scorpion species from fossil material found in Dominican amber, *Centruroides beynai* Schawaller and *Microtityus ambarensis* (Schawaller). Schawaller illustrated the trichobothria patterns of these two species in detail (Fig. 6, 1979 and Fig. 9, 1981), both clearly belonging to the typical Type A pattern, *alpha* version, although for species *C. beynai* the distal trichobothria of the fixed finger were not visible, four trichobothria being excluded. Santiago-Blay, Schawaller & Poinar (1988) named species *Tityus geratus* from this same amber. Santiago-Blay & Poinar (1993) reported a

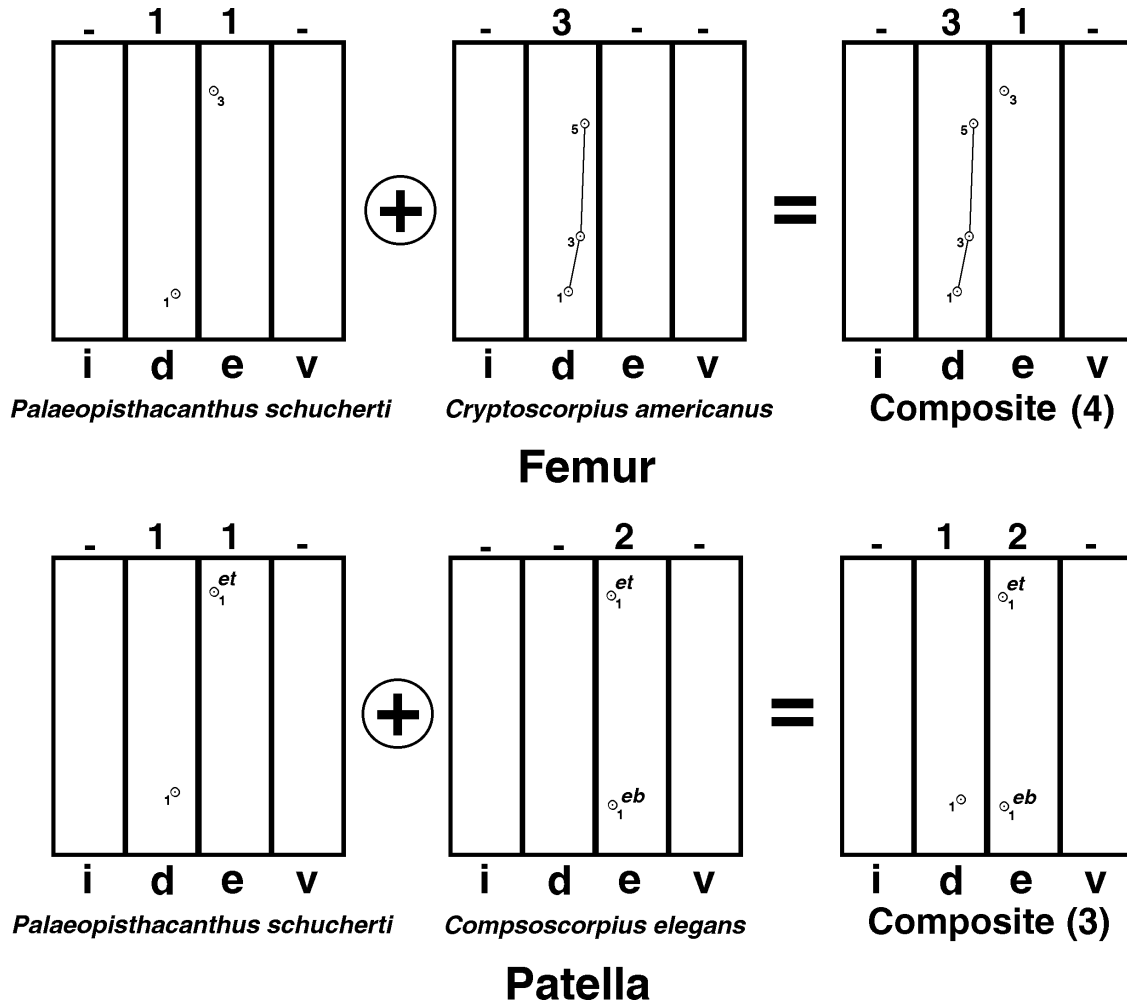


Figure 1: Hypothesized trichobothria homologies of palaeopisthacanthids for pedipalpal femur and patella based on a composite of species using *logical union*. Number of trichobothria per surface indicated on top of diagrams. *i* = internal, *d* = dorsal, *e* = external and *v* = ventral surfaces.

fossil *Centruroides* specimen from amber found in Chiapas, Mexico (Lower Miocene to Upper Oligocene, 22.5-26 Ma, minimum age). The Dominican deposits have been reported as Lower Oligocene to Upper Eocene (30-40 Ma), however, Itturalde-Vinent & MacPhee (1996) show that they are only 15-20 Ma old (i.e. Middle to Lower Miocene). To further show that these fossils belong to Recent genera, the fossil *Centruroides beynai* Schawaller was even synonymized with the extant species, *C. nitidus* (Thorell) by Armas (1988). As with the ‘palaeo-buthids’, we use these New World fossil records as ‘time-line’ data, which is discussed further.

Establishment of trichobothria homologies

We establish homologous trichobothria across six fundamental patterns. These include all five scorpion orthobothriotaxic pattern types: Type P, the palaeopis-

thacanthids (formally established in this paper, see Fig.14); Type D, the pseudochactids (formally established in this paper, see Fig. 13); Type A, the buthids; Type B, the chaerilids; and Type C, the remainder of Recent scorpions. The fossil archaeobuthids are designated here as the sixth pattern, F1. We are not establishing a formal Type for the archaeobuthids, reserving that distinction for all Recent scorpions and our oldest to date complete pattern, the palaeopisthacanthids. Otherwise, *Archaeobuthus* is included in all aspects of our cladistic analysis presented herein. Note that for Type A pattern we adopt Vachon’s *beta* pattern (1975a) as illustrated in his monumental work of 1974 (Figs. 30-36) as a ‘standard’ since it is representative of the majority of buthid genera.

Each pedipalp segment is discussed individually. For each segment we present the assigned homologies in diagrams graphically depicting the four surfaces of a

segment: internal, dorsal, external and ventral (Figs 2-4). For the chela (Fig. 2), we segregate the trichobothria into those found on the fixed finger and the palm. The numbers of trichobothria for each surface as well as the total for the segment is stated on the diagram for each pattern.

Chela (Fig 2): Jeram's (1994) data for *Palaeopisthacanthus* chela is the most complete of any of the pedipalp segments of this family and therefore it is of great importance to this analysis. We accept it *in toto* and use it as the standard Type P pattern, and, except for minor changes in individual trichobothria designations, compare it directly with the five patterns representing Recent scorpions and *Archaeobuthus*. Similarly, except for one exception, we follow Lourenço's (2001) designation for chelal trichobothria for *Archaeobuthus*, presumably a complete fossil pattern: Eb_2 and Eb_3 are changed to Eb_1 and Eb_2 . The following homologies have been established which are different from those chosen by the four original authors (Vachon, 1974; Jeram, 1994; Gromov, 1998; Lourenço, 2001): Type P: eb , Et_3 and Et_2 are changed to et , est and eb , respectively, showing consistency with Type D; Type D: Est changed to Et_1 and Em to Est , again showing consistency with the other Recent scorpion patterns; and Type A: Esb is changed to Et_4 , based on position and the petite condition of Et_4 as found in Type C (note that this change is based on comparative positions only, since it has no affect on parsimony - Types A and C exhibit, exclusively, trichobothria Esb and/or Et_4).

It is interesting to compare the chelal external patterns of Type P with those of Type D. They both have seven trichobothria in approximately the same position, with those in Type P a little more centralized around the finger/palm juncture. By repositioning the Type P pattern a little more distally and towards the dorsal aspect, we have the same pattern as exhibited in Type D. Jeram (1994, p. 526) had suggested that maybe *P. schucherti* had a third Eb trichobothrium at the base of the palm, a reference to probably the three Eb trichobothria found in Types A, B and C (note that *Pseudochactas* had not been yet described at the time of Jeram's analysis). However, we strongly suggest here, based on the absence of the Eb_3 in the Cretaceous archaeobuthids and Type D and also the petite development of Eb_3 in Type A, that the palaeopisthacanthids did not have a third Eb trichobothrium.

Another interesting observation is the lack of internal and dorsal trichobothria on the chela for Type P. Not until *Archaeobuthus* do we see two dorsal trichobothria on the fixed finger which is continued through the three presumably basal Recent scorpion types, which also exhibit one to two internal trichobothria. Only Type C has a significant number of chelal dorsal trichobothria, a total of six on the fixed finger and palm.

Probably the most surprising observation from these homology statements is that the most primitive scorpions, Type P and presumably the most recent scorpions, Type C, both have four ventral trichobothria on the palm, even with very similar distribution. The ventral pattern established for Type P is based on two different palaeopisthacanthid species (and possibly, *Compsoscorpium* as a third), so it is a very reliable set of designations. Note that even *Corniops* has at least two trichobothria on this surface. In line with this, as stated elsewhere in this paper, the New World fossil *Protoischnurus* from the Cretaceous also exhibits four ventral trichobothria on the chela.

Patella (Fig. 3): The Type P designations are based on a composite of species *P. schucherti* and *C. elegans* (see Fig. 1), otherwise designations remain as originally defined by Jeram. For the other patterns, we have altered the original trichobothria designations established for the patella in the following manner. Dorsal surface: archaeobuthids (F1): d_5 is changed to et_1 due to its external position as illustrated in Fig. 13 in Lourenço (2001); for other changes see reasons for Type A; Type A: d_2 is changed to d_5 and d_5 to d_3 , which is more consistent with Types D and B; External surface: we changed Types A, B and D designations to be more consistent with Type C, emphasizing the 'landmark' trichobothria esb_1 , est , and et_1 as emphasized by Vachon. For example both Type A and B have seven trichobothria on the external surface, and therefore we see no reason to designate them differently based on subtle positional differences as originally proposed by Vachon. Similarly Type D, a subset of Types A and B, follows this same convention. For *Archaeobuthus*, we follow Lourenço's designations except for the addition of et_1 discussed above. These homologies of the external surface are essentially self-contained and therefore their actual designations (eb_3 versus eb_4 , etc.) do not affect the outcome of the cladistic analysis. I.e., Type D contains all Type P designations, Types A and B contain Type D, and Type C contains them all.

Femur (Fig. 4): The Type P designations are based on a composite of species *P. schucherti* and *Cryptoscorpium americanus* (see Fig. 1), otherwise the basic designations remain as originally defined by Jeram (1994). The hypothesized homologies for femoral trichobothria are as originally proposed by Vachon (1974), Gromov (1998) and Lourenço (2001) with two exceptions: (1) *Archaeobuthus*: e_1 is changed to e_3 , for compatibility with Type P and D patterns; (2) we number the dorsal trichobothria for Type B as 1, 3, 4, & 5, not as 1 through 4 as originally proposed by Vachon. Since d_2 on Type A is petite, it is more efficient (least number of changes) to suggest the loss of this trichobothrium than its regaining full size and the complete loss of d_5 (1 step versus 3).

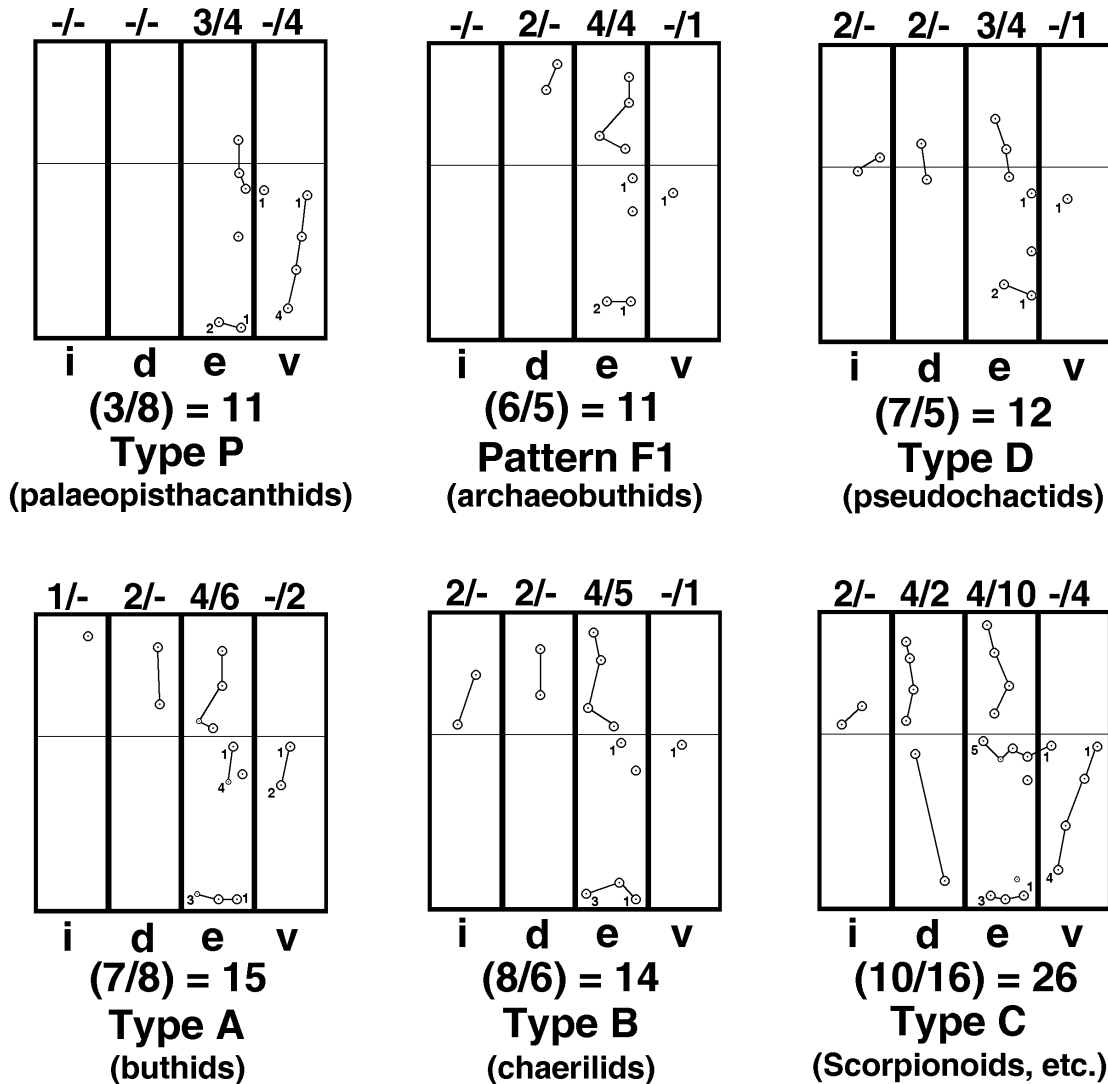


Figure 2: Hypothesized trichobothria homologies of six basic patterns for pedipalp *chela*. Diagrams split into fixed finger area, upper region, and palm area, lower region. Number of trichobothria per surface indicated on top of diagrams (fixed finger/palm). *i* = internal, *d* = dorsal, *e* = external and *v* = ventral surfaces.

Trichobothria designations: an issue of terminology

It is important to stress here that the purpose of this paper is to investigate the evolution of scorpion orthobothriotaxic patterns, *not* the consolidation of trichobothria designations across the pattern types. Although it was necessary to make minor changes, as indicated above, to specific designations in some patterns for the sake of homology, which is required for a meaningful cladistic analysis, we strongly believe in preserving the extant designations which are now widely accepted and used throughout scorpion systematics. In particular designations within Type A and Type C are particularly sensitive to arbitrary changes in designations (especially

the latter) since they exhibit by far the most diversity in hypothesized positional designations and consequently the body of work is quite large dealing with these patterns. This situation is further complicated by the significant neobothriotaxy found throughout Recent scorpions conforming to these two types. Now, having stated the above, we do propose two new orthobothriotaxic types, Type D for the pseudochactids (Fig. 13) and Type P for the palaeopisthacanthids (Fig. 14), where the trichobothria designations do deviate somewhat from those proposed by the original authors (Gromov, 1998; Jeram, 1994). Since the original designations exist in solitary papers, both of which are quite recent, and represent a minimum of taxa (five species in all), we feel these changes cause minimal if any perturbations, and

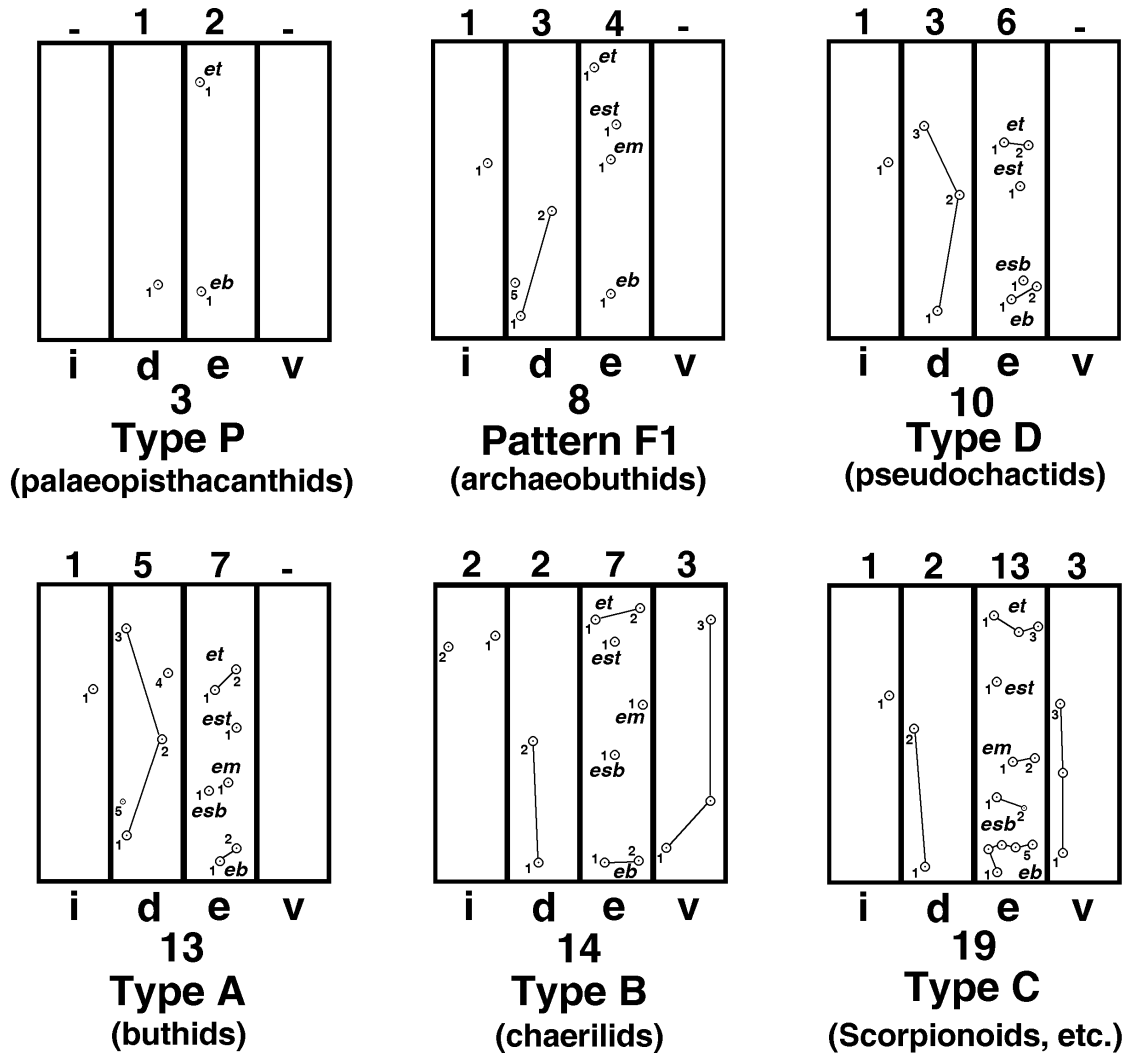


Figure 3: Hypothesized trichobothria homologies of six basic patterns for pedipalp *patella*. Number of trichobothria per surface indicated on top of diagrams. *i* = internal, *d* = dorsal, *e* = external and *v* = ventral surfaces.

therefore we are justified in making them. And finally, it should be stressed here that Vachon (1972, 1974) did not attempt to reconcile homology of trichobothria *across* his three fundamental pattern types, as he used the same positional terminology only to represent gross positions of the trichobothria. However, within a pattern, in particular Type C, where the most diversity of trichobothrial ‘movement’ is evident and where major neobothriotaxy further obscured the identity of orthobothriotaxic trichobothria, Vachon (1974) did consider individual trichobothrium homology important, as evidenced by the diversity of patterns he hypothesized.

Cladistic Analysis

We present the cladistic analysis of each pedipalp segment separately, followed by the analysis of the segments combined (‘total’ analysis, the pedipalp). The

character coding (i.e., trichobothria existence statements) is based on the homology established elsewhere in this paper. See **Appendix C** for the actual character state assignments. Each analysis sequence is conducted using the ‘exact algorithm’ (BANDB in PAUP*) with accelerated character optimization (ACCTRAN in PAUP*), thus emphasizing homoplasy as character reversals, which in this case would be the loss of a trichobothrium or the change from a full trichobothrium to a petite trichobothrium (see **Appendix B** for issues concerning trichobothria derivations based on DELTRAN and unambiguous optimizations). All uninformative characters are suppressed in each PAUP* sequence, thus support and consistency data is not inflated. However, *all* characters (i.e., trichobothria existence statements) are shown distributed on the cladograms. Each distinct sequence (four in all) was initiated eleven times in order to determine minimum, maximum and mean values for

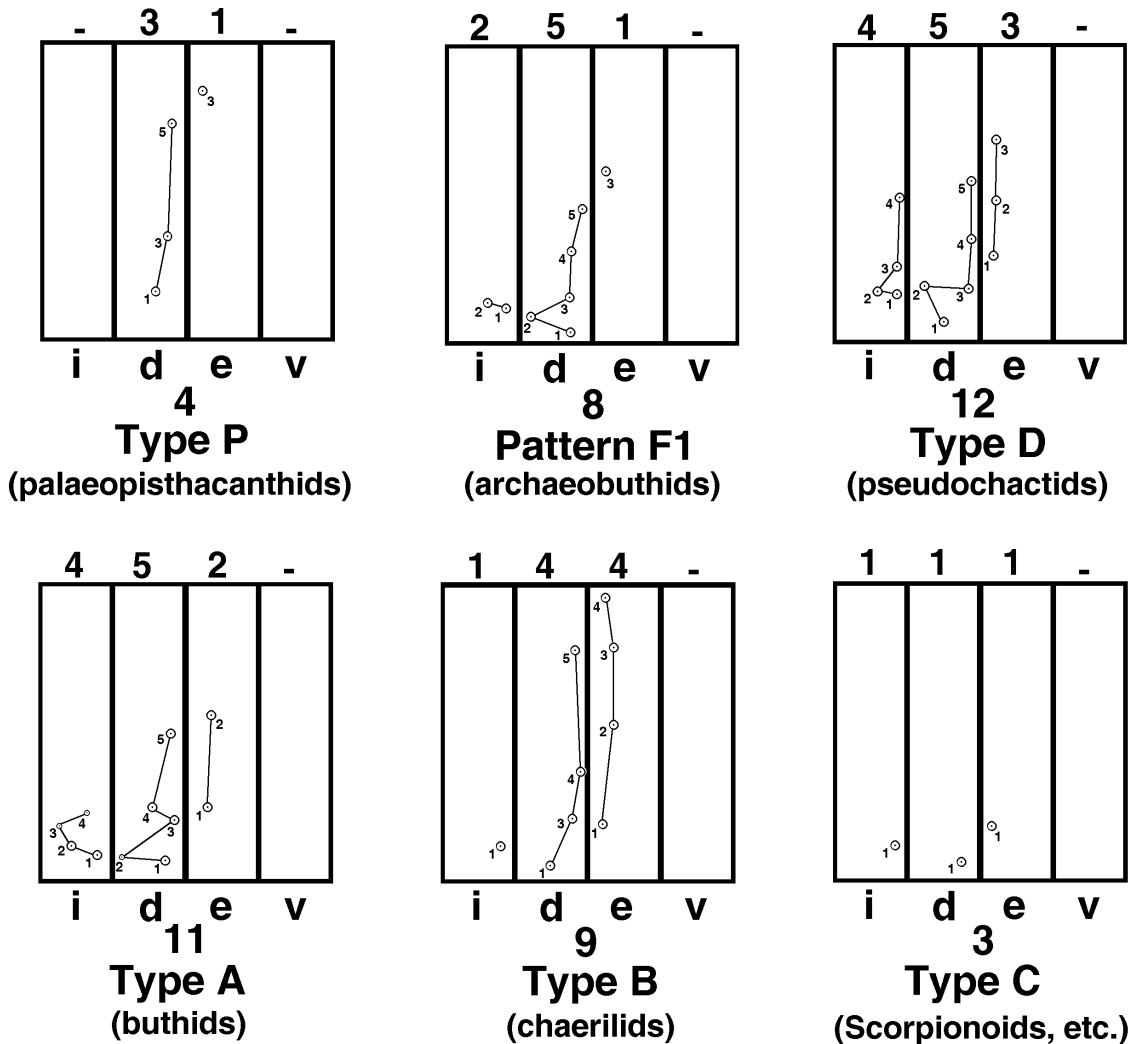


Figure 4: Hypothesized trichobothria homologies of six basic patterns for pedipalp *femur*. Number of trichobothria per surface indicated on top of diagrams. *i* = internal, *d* = dorsal, *e* = external and *v* = ventral surfaces.

the pseudoreplicate resampling data derived from both bootstrap and jackknife operations. For each sequence iteration, 1000 pseudoreplicates each were obtained per bootstrap and jackknife operation; i.e., the mean value is based on 11000 pseudoreplicates. [Note that due to the ‘randomness’ requirement of the two pseudoreplicate algorithms, significant variability is encountered in the individual support values calculated across the 88 pseudoreplicate sequences. Magnitude percentage differences between the minimum and maximum support level varied anywhere from 3 to 7, exhibiting a plus-minus error rate when compared to the mean of 2.5 to over 30%. Therefore, we exercise multiple sequences in order to dilute this error by calculating and reporting a derived mean value.] All parsimony analysis was conducted using software package PAUP* Version 4 (beta) (Swofford, 1998). Winclada Version 0.9.3 (Nixon, 1999) was used to generate, in part, the resulting PAUP* MP cladograms showing distribution of all characters (i.e., trichobothria) and their states. Additional cladogram

generation without character distribution was initiated through TreeView (Page, 1998). All cladograms with character distribution (Figs. 5 - 8) show the actual distribution of all trichobothria on the branches, their size (either full or petite), and whether they are synapomorphic or homoplasious as either a reversal (a loss) or independently derived.

Outgroup selection

Since we are dealing with the beginning of trichobothria evolution, we use an outgroup that presumably has no trichobothria, the suborder Branchioscorpionina. Although we don’t know specifically when trichobothria made their first appearance, it is clear that they probably did not exist in aquatic scorpions. In line with this thinking, Selden (1993, p. 392) considered trichobothria as a typical adaptation of terrestrial scorpions (in con-

trast to aquatic). The earliest known trichobothria in scorpions is from the Lower Carboniferous (348–338 Ma) as reported by Jeram (1989, unpublished Ph.D. dissertation), Selden & Jeram (1989, Fig. 4) and Jeram (1998, p. 28). For example, in Jeram's cladogram (Jeram, 1994, Text-Fig. 1), the existence of trichobothria is considered a synapomorphy for the infraorder Orthosterni (i.e., *Corniops* + palaeopisthacanthids + Recent scorpions) in contrast to Palaeosterni. Or using an alternative classification, as proposed by Kjellesvig-Waering (1986), we can contrast the branchioscorpionines and neoscorpionines (in part) without/with trichobothria (this classification is reflected in the cladograms). Although this outgroup can be considered an 'all-zero outgroup' since all characters involving trichobothria existence are assigned the primitive state of 'zero' (trichobothrium *absent*), it is important to note that it is not a 'hypothetical' outgroup since the branchioscorpionines did indeed exist.

Cladistic analysis results: the chela, patella, femur and pedipalp

Chela: Fig. 5 shows the resulting cladogram of the chela analysis for all six orthobothriotaxic patterns comprising 26 trichobothria existence characters, 10 of which are informative. Table 5 presents the support statistics of one of the two MPTs (most parsimonious tree). The somewhat conservative CI and RI, 0.6129 and 0.5714 (based on 12 extra steps for 19 minimum steps) illustrates the somewhat unresolved topology within the Recent scorpions. Note, only the branch separating Type P from Pattern F1 and the Recent scorpions has good bootstrap/jackknife support, 77/75%. See the section discussing resampling support for more information on this unresolved topology within the Recent scorpions for the chela.

Based on the topology shown in the cladogram, Type D appears to be the most primitive of Recent scorpions, but showing somewhat weak resampling bootstrap/jackknife support of 34/31% for Types A + B + C. Of importance to trichobothria distribution, note that *Pseudochactas* has essentially inherited most of its trichobothria from an ancestral lineage (prototypic Recent scorpions), with only the loss of trichobothrium *esb* as autapomorphic. The distribution of trichobothria on the chela is quite interesting as shown on the cladogram. Fixed finger trichobothrium *esb* exhibits the most homoplasy, primarily due to its presence in *Archaeobuthus* and all Recent scorpions except *Pseudochactas* (see Table 3 for homoplasy data of the chela). Trichobothrium *esb* also illustrates the reduction of a full trichobothrium to one that is petite (Type A). Predictively, the ventral trichobothria, in particular V_3 and V_4 , are among the most homoplasious, having been derived independently

in Type P and Type C scorpions, curiously, the most primitive and presumably the most recent derived scorpions, respectively. V_2 also exhibits the same homoplasy, since it also exists in Type A. Notice how the parsimony process makes use of the 'petite' designation of the Sankoff model used in this analysis: it correctly optimizes Et_4 joining Types A and C and establishes a petite Eb_3 (as hypothesized for Type A) and then elevates it to a full trichobothrium for Types B and C. Trichobothria *ib* and *esb* are the only trichobothrium that are lost in this analysis, the former in Type A, which is predictable, since it is present in the other three Recent scorpion types.

Patella: Fig. 6 shows the resulting cladogram of analysis of the patella for all six orthobothriotaxic patterns comprising 23 existence characters, 12 of which are informative. Table 5 presents the support statistics of the single MPT. The analysis of the patella exhibits extremely high CI and RI, 0.8889 and 0.9032 (based on only 3 extra steps for 24 minimum steps). The cladogram illustrates very strong support for *Archaeobuthus* + Recent scorpions as separated from the palaeopisthacanthids, 99/97%. Support separating *Archaeobuthus* from the Recent scorpions is also strong, 86/83%, as well as 98/93% for Types B + C and 68/60% for Types A + D.

In this cladogram the Recent scorpions are segregated into Types D + A and Types B + C pairings, all strongly supported by bootstrap/jackknife resampling. The ancestral trichobothria set occurring at the prototypic archaeobuthid node essentially represents the trichobothria for *Archaeobuthus*, with only one autapomorphic derivation occurring, the gain of trichobothrium d_5 . In Table 3 we see little homoplasy for the patella sequence, trichobothrium em_1 derived at the prototypical archaeobuthid node and then being loss on the pseudochactids. Trichobothrium d_5 is derived separately for *Archaeobuthus* and the buthids, petite for the latter. Only one trichobothrium is lost in this analysis, em_1 in Type D.

Femur: Fig. 7 shows the resulting cladogram of the analysis of the femur for all six orthobothriotaxic pattern types comprising 13 existence characters, 11 of which are informative. Table 5 presents the support statistics of the single MPT. The CI and RI, 0.6875 and 0.6774 (based on 10 extra steps for 22 minimum steps) represent modest consistency and synapomorphic potential for this character set, although a topology completely contrary to that derived by the separate analyses of the chela and patella.

In direct contradiction to the other two analyses, the trichobothria analysis of the femur suggests that Recent scorpions are not monophyletic, but instead, Type C scorpions evolved separately from the palaeopisthacanthids, archaeobuthids and other basal Recent scorpions. Although the support for patterns P + F1 + A + B + D is

Branchioscorpionina (trichobothria not present)

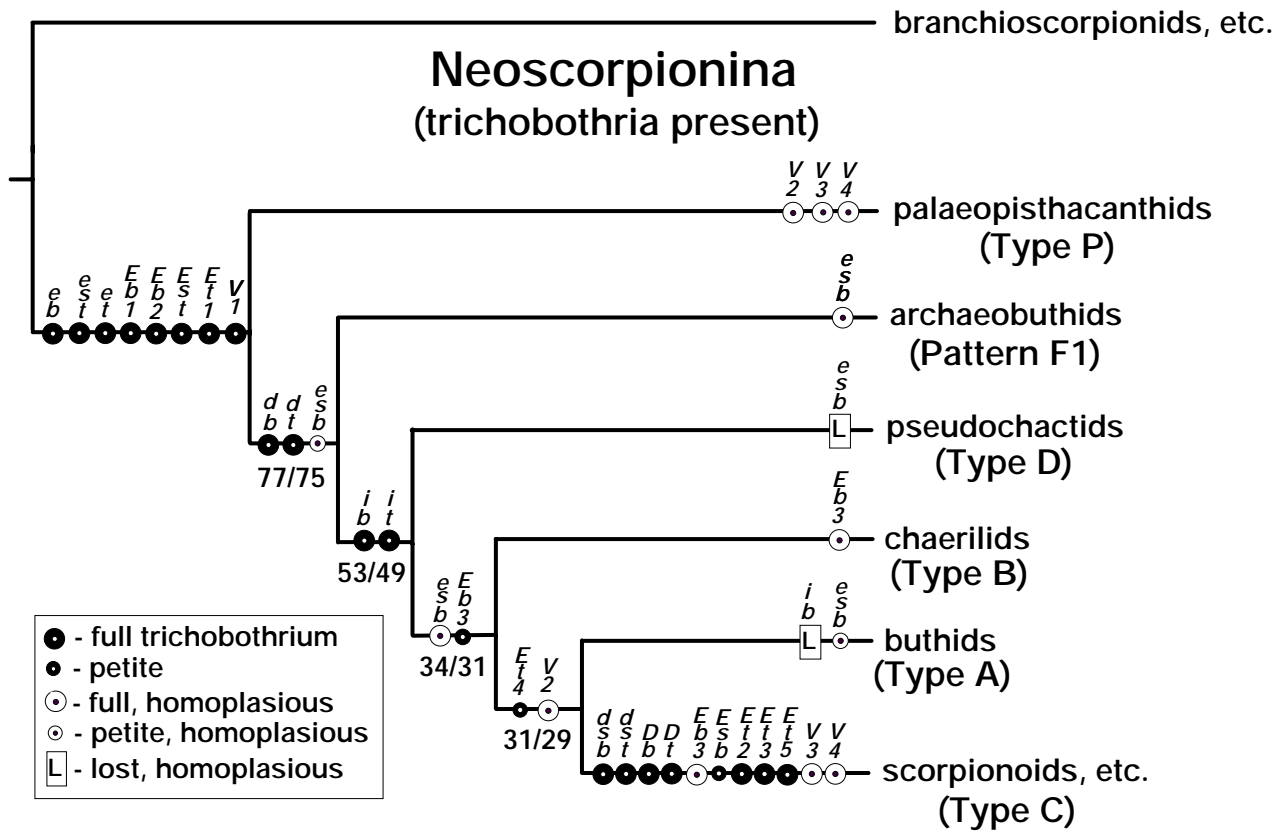


Figure 5: Cladogram showing most parsimonious (MP) distribution of *chela* trichobothria for six basic pattern types. Bootstrap/jackknife support values indicated below each branch, presented as mean values based on eleven separate resampling sequences, 1000 pseudoreplicates each.

good at 72/65%, the support data binding two of the internal subclades is weaker, 45-69%, with only D + A exhibiting good support at 76/69%.

The homoplasy for the femur (see Table 3) is considerable, only exceeded slightly by that exhibited in the chela. Five trichobothria have two extra steps in their distribution, with four trichobothria being lost, i_1 , i_2 , d_2 and e_3 .

The resulting topology of the femur analysis is not surprising, however, considering that our outgroup is a scorpion without trichobothria and the Type C scorpions have the lowest number of femoral trichobothria. The abrupt dichotomy of ‘many is primitive’ for the femur versus ‘few is primitive’ for the chela and patella is well demonstrated here with the three analyses just presented.

Pedipalp (‘total’ analysis): Fig. 8 shows the resulting cladogram of the analysis of the entire pedipalp, combining the femur, patella and chela for all six orthobothriotaxic pattern types comprising 62 trichobothria existence characters, 33 of which are informative. Table 5

presents the support statistics of the single MPT. The CI and RI, 0.6633 and 0.6333 (based on 33 extra steps for 65 minimum steps), exhibit an intermediate consistency and support result between that of the chela and the femur but much lower than that of the patella.

The topology exhibits maximum support for *Archaeobuthus* + Recent scorpions (100/100%), very strong support for Recent scorpions (92/91%), and strong to reasonable support for subclade breakdown within the Recent scorpions, Types A + D, 68/65%, and Types B + C, 88/86%. This analysis implies, taking all trichobothria into consideration, that *Pseudochactas* is more closely related to the buthids than it is to the chaerilids. We discuss this issue further in the final comments of this paper.

The distribution of trichobothria on branches terminating at individual pattern types (i.e., autapomorphies) is quite interesting, especially when contrasted with distributions as exhibited by the individual analyses presented above:

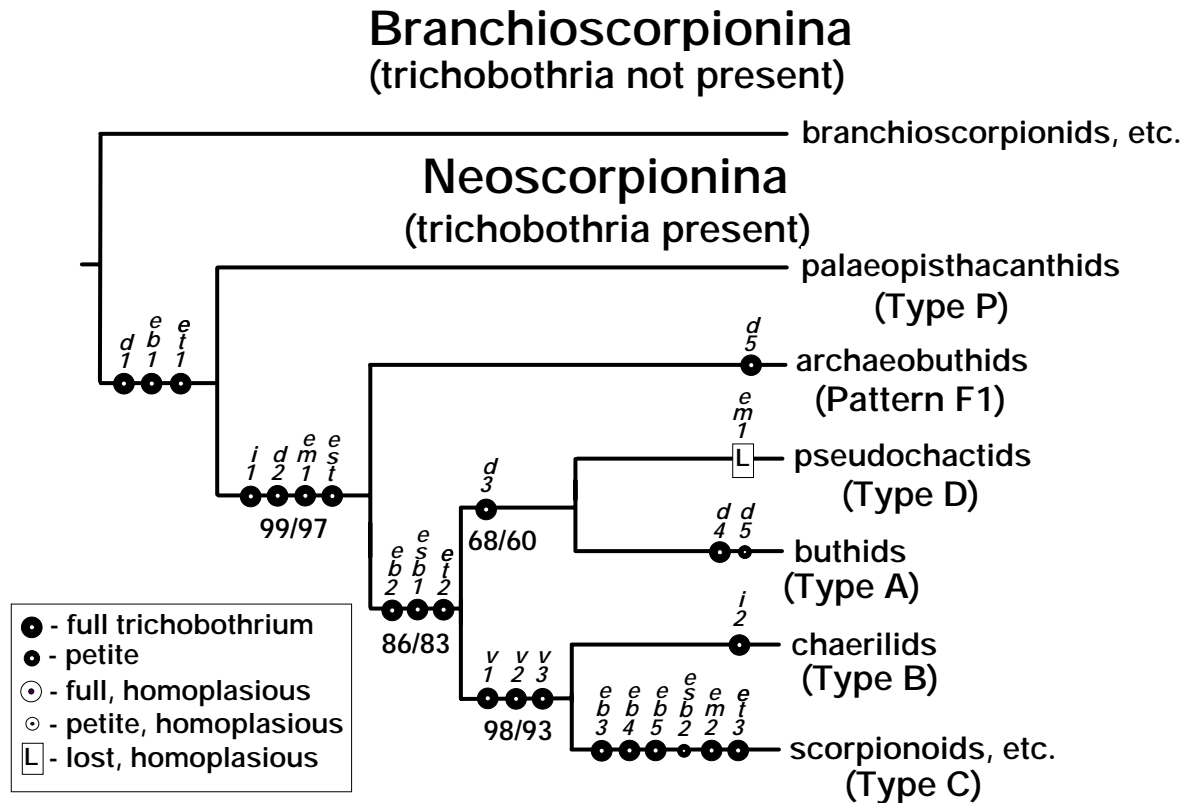


Figure 6: Cladogram showing most parsimonious (MP) distribution of *patella* trichobothria for six basic pattern types. Bootstrap/jackknife support values indicated below each branch, presented as mean values based on eleven separate resampling sequences, 1000 pseudoreplicates each.

Type C: the distribution is as expected: for the femur there is massive loss of trichobothria, no less than five; for the patella and chela, there is the derivation of 18 trichobothria (15 full and three petite), of which 14 are autapomorphic. In comparison with the individual analyses by segment, only the loss of femoral trichobothria is in significant odds with the analysis based on the femur alone. In the latter, two trichobothria were gained. This pattern of loss/gain for Type C scorpions is certainly consistent for a group of presumed recently derived taxa with the dynamics of an all-zero outgroup and the ‘many’ versus ‘few’ is primitive hypotheses in play.

Type B: three derivations are found in this analysis, two for the femur and one for the patella. In comparison with separate segment analysis, only the femur shows the most deviation, two derivations versus three, and the chela, no derivations versus one.

Type A: the femur and patella are identical for both sets of analyses, including the single trichobothrium loss for the femur; the chela derived two trichobothria, one petite, both homoplasious and exhibited one loss whereas in the single analysis, a loss and a gain were present.

Type D: with respect to derivations, the pedipalp analysis matched the individual analyses for the femur

and patella. The chela exhibited an extra gain, *ib*, and another loss, *Eb*₃, from the original analysis.

Pattern F1: the autapomorphic derivations of the pedipalp are identical to those exhibited in the individual analyses.

Type P: derivations are almost identical for the palaeopisthacanthids whether total analysis or separate: Type P lost one trichobothria in the separate analysis of the femur in contrast to none for the total analysis.

To summarize trends from the above: the total analysis involved more trichobothria losses than the separate analyses, twelve versus seven; the number of autapomorphic derivations was quite close, 35 (14 homoplasious) versus 34 (13 homoplasious) for the separate analyses. It is also interesting to note that homoplasy does not occur on any of the three archetypic ancestral nodes, only first appearing on subclades involving the Recent scorpions. Also, each taxon exhibits autapomorphic homoplasy to one degree or another.

Homoplasy

Homoplasy comparison of individual segments in the pedipalp analysis with those same segments when analyzed separately is quite interesting (compare Tables 3

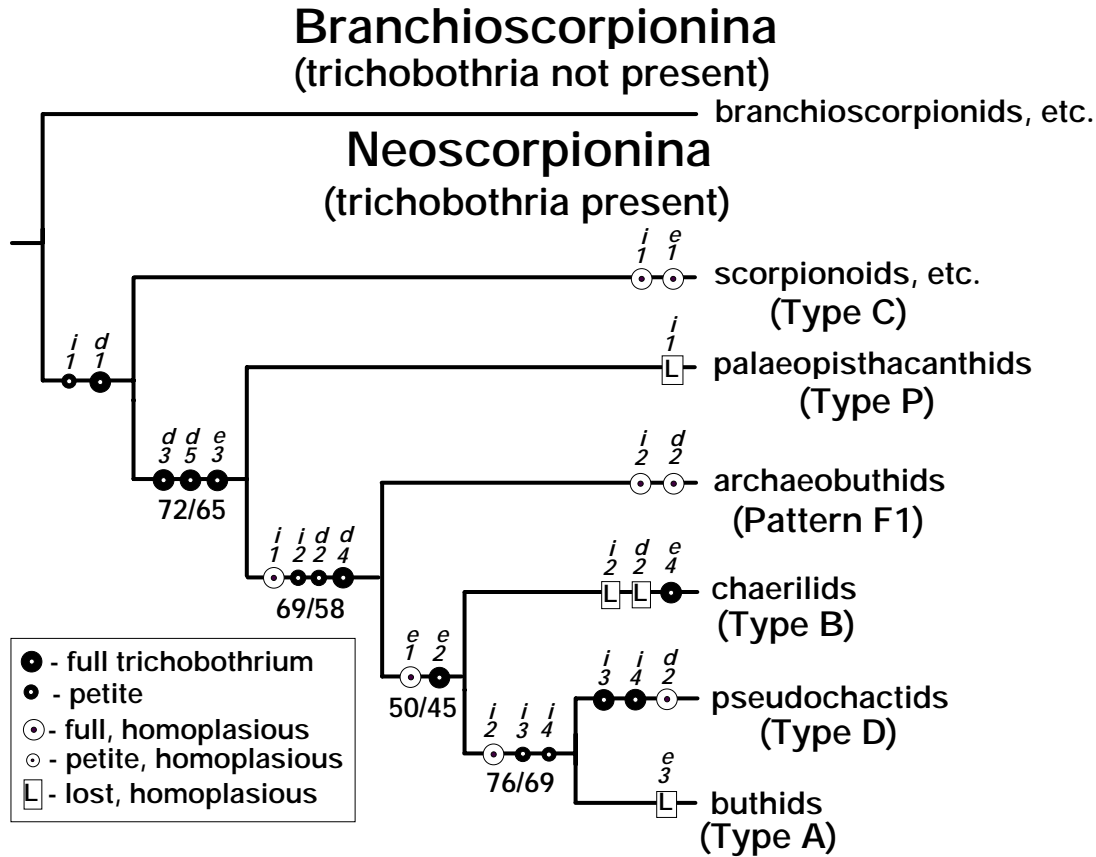


Figure 7: Cladogram showing most parsimonious (MP) distribution of *femur* trichobothria for six basic pattern types. Bootstrap/jackknife support values indicated below each branch, presented as mean values based on eleven separate resampling sequences, 1000 pseudoreplicates each.

and 4). First important observation is that the patella exhibited the same set of consistency and support data in both sets of analyses, three extra steps and the same trichobothria are homoplasious, d_5 and em_1 . This result is also supported by comparing individual autapomorphic characters across all six types for the four sets of analyses where they corresponded exactly. For the femur and chela, the total analysis represented by the pedipalp showed considerable more homoplasy, the number of homoplasious characters increased from 5 to 7 on the femur, 16 extra steps versus 10, with a G-Fit of 7.643 versus 9.000; and from 6 to 7 for the chela, 14 extra steps versus 12, with a G-Fit of 7.329 versus 7.729. With the femur the actual trichobothria involved in the homoplasy changed from the separate analysis to the total analysis, while i_2 , d_2 and e_3 were the only trichobothria that were consistent across both analyses. Also noteworthy is the decrease in individual character fits from the separate analysis to the total analysis. For the femur trichobothrium e_3 G-Fit decreased from 0.600 to 0.429 (two extra steps to four extra steps). Similarly, chelal trichobothrium V_2 G-Fit decreased from 0.600 to 0.429. These two trichobothria are the most homopla-

sious characters of the entire set. Analyzing homology from the point of view of congruency, one might question the true homology of that proposed for femoral e_3 and chelal V_2 trichobothria. Note that in addition to a low CI, both trichobothria have zero RI, thus no synapomorphic potential. Other trichobothria exhibiting zero RI are d_3 and d_5 of the femur, d_5 of the patella, and Et_4 and V_3-V_4 of the chela.

Bootstrap/jackknife support

Table 6 presents the bootstrap/jackknife support statistics for all important clades based on the four separate analysis sequences conducted in this study. As discussed above, the trichobothrial patterns of the chela, patella, femur, and the pedipalp (a combination of the three segments) are analyzed separately in order to ascertain phylogenetic trends on a segment by segment basis. The ‘consensus’ is an averaging of the support data taken from the four analyses, both bootstrap and jackknife, thus including eight support data samples per clade. Presented bootstrap and jackknife support values are

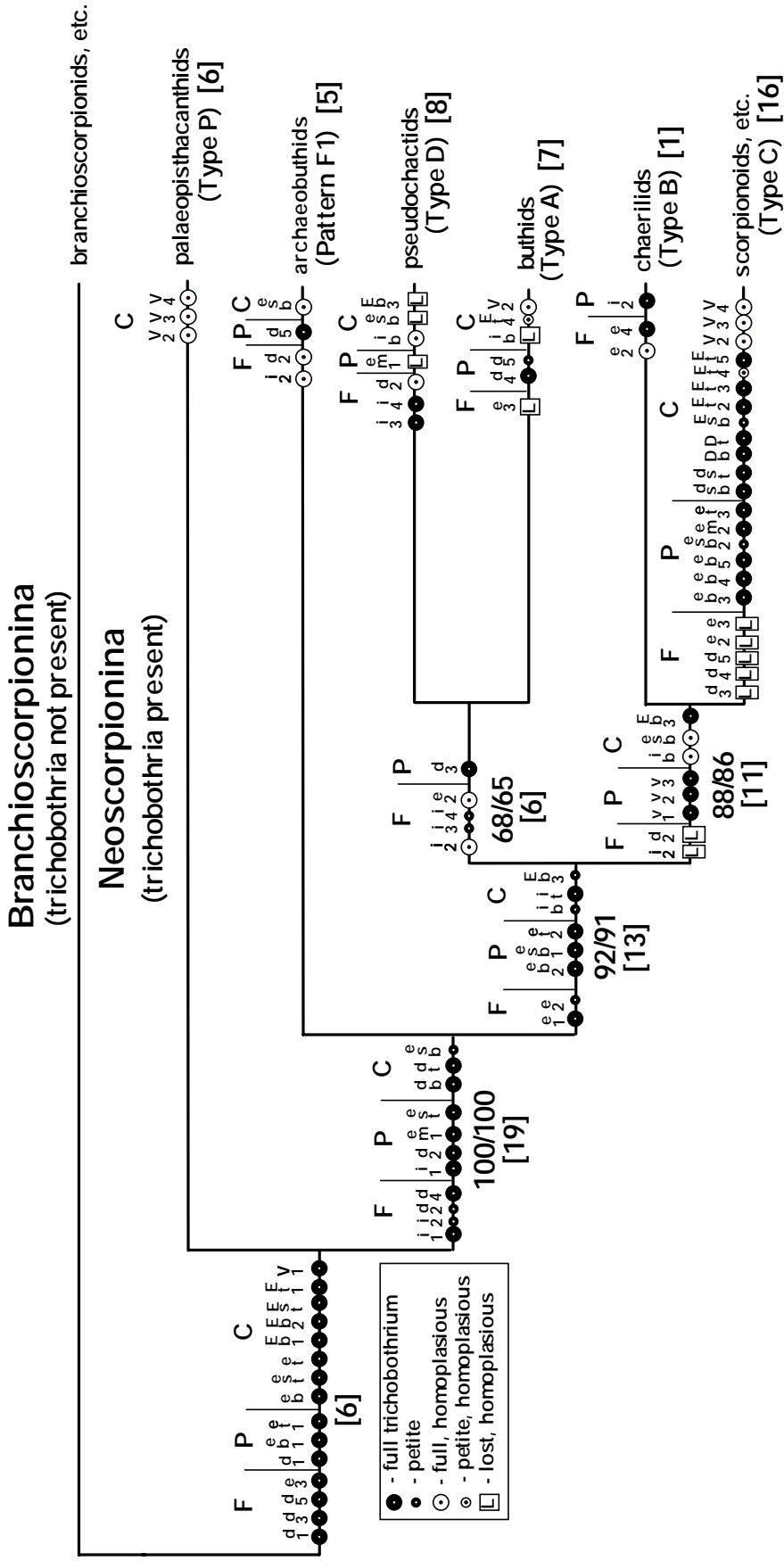


Figure 8: Cladogram showing most parsimonious (MP) distribution of *pedipalp* trichobothria (total analysis) for six basic pattern types. Trichobothria segregated on branch by segment: F = femur, P = patella, C = chela. Bootstrap/jackknife support values indicated below each branch, presented as mean values based on eleven separate resampling sequences, 1000 pseudoreplicates each; branch length based on informative characters indicated below each branch inside square brackets [...].

| Trichobothrium | Length | Extra Steps | CI | RI | RC | G-Fit (k = 2) |
|---|--------|-------------|-------|-------|-------|---------------|
| Femur (CI/RI/G-Fit = 0.6875/0.6774/9.000) | | | | | | |
| <i>i</i> ₁ | 4 | +2 | 0.500 | 0 | 0 | 0.600 |
| <i>i</i> ₂ | 4 | +2 | 0.500 | 0.500 | 0.250 | 0.600 |
| <i>d</i> ₂ | 4 | +2 | 0.500 | 0.333 | 0.167 | 0.600 |
| <i>e</i> ₁ | 4 | +2 | 0.500 | 0.500 | 0.250 | 0.600 |
| <i>e</i> ₃ | 4 | +2 | 0.500 | 0.500 | 0.250 | 0.600 |
| Patella (CI/RI/G-Fit = 0.8889/0.9032/11.350) | | | | | | |
| <i>d</i> ₅ | 3 | +1 | 0.667 | 0 | 0 | 0.750 |
| <i>em</i> ₁ | 4 | +2 | 0.500 | 0.500 | 0.250 | 0.600 |
| Chela * (CI/RI/G-Fit = 0.6129/0.5714/7.729) | | | | | | |
| <i>ib</i> | 4 | +2 | 0.500 | 0.500 | 0.250 | 0.600 |
| <i>esb</i> | 5 | +3 | 0.400 | 0.250 | 0.100 | 0.500 |
| <i>Eb</i> ₃ | 3 | +1 | 0.667 | 0.667 | 0.444 | 0.750 |
| <i>V</i> ₂ | 4 | +2 | 0.500 | 0.500 | 0.250 | 0.600 |
| <i>V</i> ₃ | 4 | +2 | 0.500 | 0 | 0 | 0.600 |
| <i>V</i> ₄ | 4 | +2 | 0.500 | 0 | 0 | 0.600 |

Table 3: Homoplasious character statistics for the femur, patella and chela analyzed *individually*. Consistency and character fit data (CI, RI and G-Fit) is presented for each analysis. CI = consistency index, RI = retention index, RC = rescaled consistency index, G-Fit = Goloboff fit (see Kitching *et al.*, 1998, for definitions). * Homoplasia data for chela is from one of two isolated MPT's.

derived as the mean of eleven separate resampling sequences, each isolating 1000 pseudo-replicates, a total of 11000 replicates for each data. Therefore, each 'consensus' data is based on 88000 pseudoreplicates involving 88 separate sequences.

Chela: The most significant support derived from this analysis was for the archaeobuthids + Recent scorpions, exhibiting 77/75 bootstrap/jackknife support, followed by the Recent scorpions, 53/49. As shown in the cladogram (Fig. 5), Type D is separated from the other recent scorpions, exhibiting a somewhat weak support, 34/31. Particular type pairings were weak in this analysis as compared to the other three analyses. As shown in Fig. 5, bootstrap/jackknife resampling gave a support of 31/29 for Type A + Type C, and, for a clade shown in the alternative MPT, the MP analysis grouped Type B + Type C with a support of 47/44. Interestingly, the analysis of the chela was the only analysis that exhibited any support for a coupling of the palaeopisthacanthids (Type P) and a recent type, Type C. The support was quite low however, 18/17. This support is caused in most part by the four ventral trichobothria present in both types (see Fig. 5).

Patella: As with the chela, the highest support in this analysis was for archaeobuthids + Recent scorpions, showing a 99/97 support for this clade, again followed by strong support for the Recent scorpions, 86/83. Two

important type pairings were supported, Types B + C, 98/93 support, and Types D + A, 68/60 support. This analysis shows a closer affinity for Type D scorpions with Type A. In this analysis, the clade *Archaeobuthus* + buthids was the highest of the four, but only exhibited a very limited 11/12 support.

Femur: As discussed elsewhere, the femur trichobothria analysis is the only analysis which implies Recent scorpions are not monophyletic, exhibiting strong support for the basal Recent scorpions and fossil scorpions, palaeopisthacanthids and archaeobuthids, 72/65 (i.e., excluding Type C scorpions). In contrast to the other analyses, support for all Recent scorpions (including Type C) is very low at 12/14. The only strong type pairing is that of Type D + Type A, a support of 76/69, a common theme in this analysis.

Pedipalp: Pedipalp analysis (the combination of the previous three analyses) shows maximum support for *Archaeobuthus* + Recent scorpions, 100/100, and 92/91 for Recent scorpions. Important type pairings are Types D + A, a support of 68/65, and Types B + C, a support of 88/86.

Consensus: Computing a 'consensus' of the four analyses (i.e., averaging the eight support sequences for each clade, 88000 replicates in all), we have strong overall support for four clades: *Archaeobuthus* + Recent scorpions, 75.75; Recent scorpions, 60; and reasonable

| Trichobothrium | Length | Extra Steps | CI | RI | RC | G-Fit (k = 2) |
|---|--------|-------------|-------|-------|-------|---------------|
| Femur (CI/RI/G-Fit = 0.5789/0.4839/7.643) | | | | | | |
| <i>i</i> ₂ | 4 | +2 | 0.500 | 0.500 | 0.250 | 0.600 |
| <i>d</i> ₂ | 4 | +2 | 0.500 | 0.333 | 0.167 | 0.600 |
| <i>d</i> ₃ | 4 | +2 | 0.500 | 0 | 0 | 0.600 |
| <i>d</i> ₄ | 4 | +2 | 0.500 | 0.500 | 0.250 | 0.600 |
| <i>d</i> ₅ | 4 | +2 | 0.500 | 0 | 0 | 0.600 |
| <i>e</i> ₂ | 4 | +2 | 0.500 | 0.500 | 0.250 | 0.600 |
| <i>e</i> ₃ | 6 | +4 | 0.333 | 0 | 0 | 0.429 |
| Patella (CI/RI/G-Fit = 0.8889/0.9032/11.350) | | | | | | |
| <i>d</i> ₅ | 3 | +1 | 0.667 | 0 | 0 | 0.750 |
| <i>em</i> ₁ | 4 | +2 | 0.500 | 0.500 | 0.250 | 0.600 |
| Chela (CI/RI/G-Fit = 0.5758/0.5000/7.329) | | | | | | |
| <i>ib</i> | 4 | +2 | 0.500 | 0.500 | 0.250 | 0.600 |
| <i>esb</i> | 4 | +2 | 0.500 | 0.500 | 0.250 | 0.600 |
| <i>Eb</i> ₃ | 3 | +1 | 0.667 | 0.667 | 0.444 | 0.750 |
| <i>Et</i> ₄ | 2 | +1 | 0.500 | 0 | 0 | 0.750 |
| <i>V</i> ₂ | 6 | +4 | 0.333 | 0 | 0 | 0.429 |
| <i>V</i> ₃ | 4 | +2 | 0.500 | 0 | 0 | 0.600 |
| <i>V</i> ₄ | 4 | +2 | 0.500 | 0 | 0 | 0.600 |

Table 4: Homoplasious character statistics for the pedipalp (total analysis of the femur, patella and chela). Consistency and character fit data (CI, RI and G-Fit) is extracted and presented for each segment for comparison with same data in Table 3. See Table 3 for definition of terms.

support is exhibited for the two dominant type pairings, Types D + A with 50.75 support and Types B + C with 57.375 support. These four consensus ratings encompassing eight sets of pseudoreplicate sequences is consistent with and endorses the four major clades represented in the cladogram for the pedipalp (Fig. 8).

Constrained parsimony analysis

Using the results from the ‘total analysis’ of the pedipalp, we tested several other topologies in a ‘constrained parsimony’ environment. That is, we forced (i.e., constrained) an alternative topology in the context of the complete trichobothria character existence dataset. If the topology differs from that derived from the analysis of the pedipalp (Fig. 8), then it is not the most parsimonious interpretation of the data and therefore the consistency and other overall support data will be reduced. We measure these reductions in support thus establishing a relative metric to evaluate these alternative topologies. Large reductions in support are indicative of unlikely topologies, whereas minor reductions in support may represent a viable alternative topology.

Fig. 9 shows six alternative topologies that were compared with the MPT derived from the pedipalp. Of particular interest, we tested the suggested phylogenetic relationships imposed on Pseudochactidae and Archaeobuthidae by Lourenço (2000, 2001). For the former, Lourenço placed Pseudochactidae in the superfamily Chaeriloidea, accompanying the only other family Chaerilidae, a proposal based evidently on biogeographical reasons (both these families are found in Asia): Chaeriloidea = Chaerilidae + Pseudochactidae. In the latter, Lourenço (2001) placed the fossil family Archaeobuthidae in the superfamily Buthoidea: Buthoidea = Archaeobuthidae + Buthidae + Microcharmidae. These two hypotheses are tested together, creating three possible relationships with the remaining Recent scorpion orthobothriotaxic group (i.e., scorpions conforming to pattern Type C). Also of interest, we tested a slight alternative to the topology derived from the pedipalp (Fig. 8) as well as topologies derived from the individual analyses of the femur and chela (Figs. 5 & 7). Note, since the topology derived from the patella (Fig. 6) is identical to that exhibited by the pedipalp, constrained analysis serves no purpose in this case.

Table 7 shows the results of this constrained analysis. The combined two topologies proposed by Lourenço

| | Minimum Steps | Maximum Steps | Length (steps) | Number of MPTs | CI | RI | RC | G-Fit (k = 2) |
|-----------------|---------------|---------------|----------------|----------------|-------|-------|-------|---------------|
| Chela | 19 | 47 | 31 | 2 | .6129 | .5714 | .3502 | -7.729 |
| Patella | 24 | 55 | 27 | 1 | .8889 | .9032 | .8029 | -11.350 |
| Femur | 22 | 53 | 32 | 1 | .6875 | .6774 | .4657 | -9.000 |
| Pedipalp | 65 | 155 | 98 | 1 | .6633 | .6333 | .4201 | -26.707 |

Table 5: Most Parsimonious Tree (MPT) statistics (uninformative characters are suppressed). See Table 3 for definition of terms.

(we test three possible versions) increased the number of steps by 20-22 steps (an increase of over 21% in steps), a reduction in CI/RI/G-Fit of 17-18/35-39/14-16%! This significant reduction in overall support is not surprising since Lourenço's suggested phylogenies involving *Archaeobuthus* and *Pseudochactas* are not even close to that indicated in our total analysis results involving the pedipalp (Fig. 8). In our analysis *Archaeobuthus* combines completely outside all Recent scorpions, whereas Lourenço (2001) places it inside the Recent scorpions next to the buthids (in our analysis, 'buthids' = Buthidae + Microcharmidae); *Pseudochactas* is combined with the buthids in our results whereas Lourenço combines it with the chaerilids. The alternative *Pseudochactas* grouping topology, which proposes that all 'basal' recent scorpions are the sister group to Type C scorpions, only increased the number of steps by five, a decrease in CI/RI/G-Fit of 4.9/8.8/3.6% --- the pedipalp results suggest that the chaerilids are the sister group to Type C scorpions. Constraining the original chela based topology against the entire trichobothria character set increased the number of steps by nine, a decrease in CI/RI/G-Fit of 8.4/15.8/7%. The femur by far faired the worst --- an increase of 26 steps, a reduction of 21/45.6/17.2% in CI/RI/G-Fit. This decrease in support is to be expected since the 'many is primitive' dynamic of the femur is in direct conflict with the 'few is primitive' dynamic exhibited by the patella and chela (i.e., the patella + chela represent approximately twice as many character derivations as the femur alone).

Discussion

Evolution of orthobothriotaxic patterns

Prototypic Patterns: Cladistic analysis considering all trichobothria for the pedipalp (Fig. 8) is the best explanation for the dichotomous 'gain/loss' of fundamental trichobothria in Recent scorpions, as that exhibited in the chela and patella (i.e., gain) and the femur (i.e., loss). To support this analysis (see Figs. 10-11) we propose five ancestral orthobothriotaxic patterns, each one representing an internal node in the cladogram presented in Fig. 8: (1) 'proto-P', representing archetypic palaeopis-

thacanthids, (2) 'proto-F1', prototypic archaeobuthids, (3) 'proto-Recent', prototypic Recent scorpions, (4) 'proto-DA', and (5) 'proto-BC', representative of two primary subclades within Recent scorpions. Note that these patterns are derived by establishing the trichobothria as distributed on the cladogram for the pedipalp (Fig. 8). For example, in the archetypic palaeopis- thacanthids we include the 15 trichobothria on that node (four femur, three patella and eight chela); for the prototypic archaeobuthids, we add to these 15 trichobothria, 11 additional trichobothria occurring on that node, giving us a total of 26 trichobothria, eight femoral, seven on the patella, and 11 on the chela; for prototypic Recent scorpions, we add in the eight trichobothria distributed on that node, a total of 34 trichobothria (ten femur, ten patella and 14 chela); and so on. It is interesting to point out here that Jeram (1994, p. 521) proposed an ancestral pattern of the chela for Recent scorpions that included eighteen trichobothria: all fourteen trichobothria designated in our Fig. 10 plus *Esb* and $V_2 - V_4$. This pattern was obviously based on his analysis of fossil trichobothrial patterns but the actual algorithm used to determine this set of designations was not disclosed. And, of course, Jeram did not have the 'intermediate fossil' *Archaeobuthus* or *Pseudochactas* to consider.

It is important to note, since all taxa termination points (i.e., terminal nodes) exhibited autapomorphy to one degree or another, that these five ancestral patterns exhibit differences from the terminal nodes, in most cases a more primitive pattern; that is, a pattern with either fewer trichobothria or a pattern that exhibits petite states of the same trichobothrium (compare the hypothesized ancestral patterns to those homology-based patterns stated in Figs. 2-4). Exceptions to this are: the chela, *Pseudochactas* loses two trichobothria, *esb* and *Eb3*; the patella, *Pseudochactas* loses *em1*; and the femur, the buthids loses *e3*, and Type C scorpions, with a loss of five trichobothria, *d3-d5* and *e2-e3*. In the 'proto-BC' ancestral pattern we see ventral trichobothria for the first time on the patella, v_1-v_3 , absent on the prototypic Recent scorpion pattern. The reduction of internal femoral trichobothria occurs on the 'proto-BC' pattern, whereas it increases on the 'proto-DA' pattern, both a deviation

| | Chela | Patella | Femur | Pedipalp | Consensus |
|--|--------------|--------------|--------------|----------------|----------------|
| P+F | -/- | -/- | 7/10 | -/- | 2.125 |
| P+A | -/- | -/- | -/- | -/- | 0.000 |
| P+B | -/- | -/- | 3/5 | -/- | 1.000 |
| P+C | 18/17 | -/- | -/- | -/- | 4.375 |
| P+D | -/- | -/- | -/- | -/- | 0.000 |
| F+A | 3/4 | 11/12 | -/- | -/- | 3.750 |
| F+B | 5/6 | -/- | -/- | -/- | 1.375 |
| F+C | -/- | -/- | -/- | -/- | 0.000 |
| F+D | -/3 | -/- | 18/20 | -/- | 5.125 |
| A+B | -/- | -/- | -/3 | -/- | 0.375 |
| A+C | 31/29 | -/- | -/- | 3/4 | 8.375 |
| A+D | -/- | 68/60 | 76/69 | 68/65 | 50.750* |
| B+C | 47/44 | 98/93 | -/3 | 88/86 | 57.375* |
| B+D | 14/16 | -/- | 2/5 | -/- | 4.625 |
| C+D | -/3 | -/- | -/- | -/- | 0.375 |
| F+A+B+C+D (arch+recent) | 77/75 | 99/97 | 27/31 | 100/100 | 75.750* |
| A+B+C+D (recent) | 53/49 | 86/83 | 12/14 | 92/91 | 60.000* |
| P+F+A+B+D (fossil+recent_basal) | -/- | -/- | 72/65 | -/- | 17.125 |
| F+A+B+D (arch+recent_basal) | -/- | -/- | 69/58 | -/- | 15.875 |
| A+B+D (recent_basal) | -/- | -/3 | 50/45 | 8/10 | 14.500 |
| A+B+C (recent, sans Type D) | 34/31 | 10/14 | -/- | 9/9 | 13.375 |
| F+A+D | -/- | -/- | 41/40 | 6/6 | 11.625 |
| B+C+D | 31/33 | 9/12 | -/- | 21/23 | 16.125 |

Table 6: Bootstrap/jackknife support for major clades based on trichobothrial analysis of chela, patella, femur and 'total analysis', the pedipalp. Bootstrap and jackknife values (%) expressed as mean value of eleven sequences of 1000 pseudoreplicates each (11000 replicates each for bootstrap and jackknife). *Consensus* (%) is mean value of all eight bootstrap/jackknife sequences per clade (44000 replicates per bootstrap and jackknife). A = Type A (buthids), B = Type B (chaerilids), C = Type C (scorpionoids, etc.), D = Type D (pseudochactids), F = Pattern F1 (archaeobuthids), P = Type P (palaeopisthacanthids). Recent = recent scorpions; recent_basal = presumed primitive recent scorpions, Types A, B and D; fossil = archaeobuthids + palaeopisthacanthids (Pattern F1 & Type P); arch = archaeobuthids. * Significant support, consensus > 50%.

from the 'proto-Recent' scorpion ancestral pattern shown in Fig. 10.

In **Appendix B** we present 'trichobothria derivation maps' for all 62 orthobothriotaxic trichobothria hypothesized in this paper. As reflected in the homology statements presented in Figs. 2-4 and the ancestral archetypic patterns stated in Figs. 10-11, these derivation maps (one for each pedipalp segment) show the derivation of each trichobothrium for all internal and terminal nodes (eleven in all) presented in the pedipalp cladogram (Fig. 8). See the **Appendix** for an explanation on how to interpret these maps.

Evolutionary time-line considerations: Figure 12 presents the six orthobothriotaxic patterns distributed on an evolutionary time-line with respect to total trichobothria counts of the three pedipalp segments. As can be seen from the chart, in general, the trichobothria gradually increase in number from its beginning, presumably with

the palaeopisthacanthids some 290 million years ago with only 18 trichobothria, to the most recently derived lineage, Type C pattern scorpions exhibiting 48 trichobothria. This increase of trichobothria is also reflected in the chela and patella segments for the entire time-line, from the Upper Carboniferous to Recent times. And the femur, in part, also complies, its largest counts being found on Type D (the pseudochactids), but then drastically reduces on the other three Recent scorpion types, in particular, the most recently derived scorpion group, Type C (only three trichobothria are present on the femur). It is interesting to note that the pseudochactids show the most equilibrium in counts for the three segments, only two trichobothria separate the smallest and largest counts across the three segments. In contrast, Type C scorpions exhibit the least equilibrium, exhibiting a 6-23 count difference between the three segments. Also of interest, the Type A pattern, representative of the

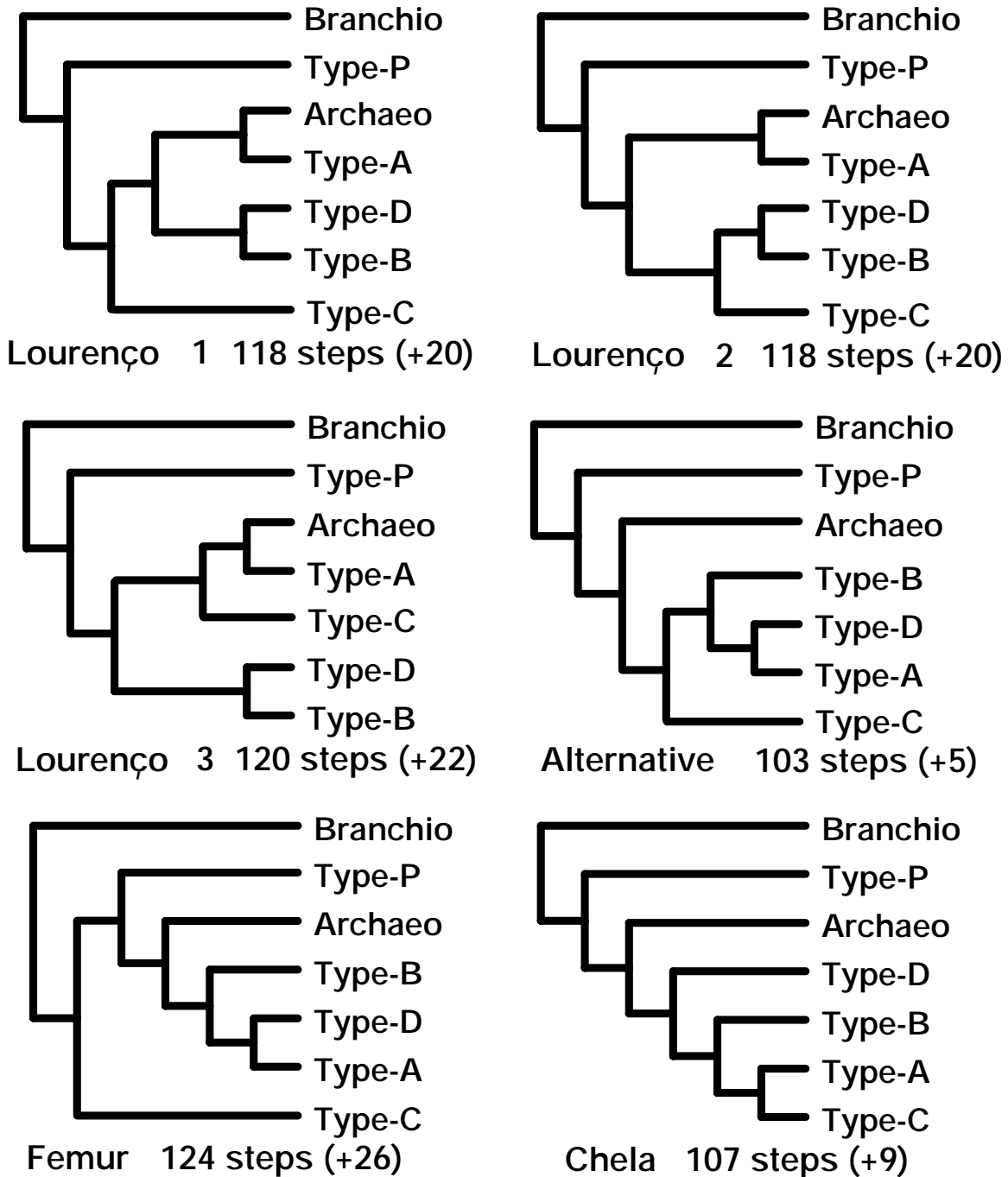


Figure 9: Constrained parsimony analysis as contrasted with original MP analysis of the pedipalp. Proposed topology of Lourenço (2000, 2001) Type A + *Archaeobuthus* and Type B + Type D showing three possible couplings with Type C, 20-22 extra steps; alternative topology, Type B + (Type A + Type D), 5 extra steps; original *femur* topology, 26 extra steps; original *chela* topology, 9 extra steps.

buthids, is found in its entirety in the Old World at least 55 million years ago, in the Eocene (based on the 'palaeo-buthids'). One can imply from this that the common ancestor of the buthids and *Pseudochactas*, exemplified by the 'proto-DA' pattern (Fig. 11), existed no

later than 55 MA. New World buthid patterns complying to typical Type A existed at least 15-20 million years ago, those occurring in Dominican amber. The limited data from the New World Cretaceous protoischnurids imply that the four trichobothria of the chelal ventral as-

| Topology | Steps (extra) | CI | RI | G-Fit | CI/RI/G-Fit Reduction (%) |
|--------------------------|---------------|--------|--------|---------|---------------------------|
| Lourenço, 1 | 118 (+20) | 0.5508 | 0.4111 | -22.907 | 17/35.1/14.2 |
| Lourenço, 2 | 118 (+20) | 0.5508 | 0.4111 | -22.907 | 17/35.1/14.2 |
| Lourenço, 3 | 120 (+22) | 0.5417 | 0.3889 | -22.507 | 18.3/38.6/15.7 |
| Alternative | 103 (+5) | 0.6311 | 0.5778 | -25.757 | 4.9/8.8/3.6 |
| Original femur | 124 (+26) | 0.5242 | 0.3444 | -22.114 | 21/45.6/17.2 |
| Original chela | 107 (+9) | 0.6075 | 0.5333 | -24.829 | 8.4/15.8/7 |
| Original pedipalp | 98 (-) | 0.6633 | 0.6333 | -26.707 | -/- |

Table 7: Constrained parsimony analysis. Comparison of alternative topologies with most parsimonious topology derived from the pedipalp ('total' analysis). See Fig. 8 for original topology derived from pedipalp, Fig. 9 for six constrained topologies as defined in table, and Table 3 for definition of terms.

pect found in Type C scorpions was present at least 110 million years ago, which would imply that the 'proto-BC' ancestral pattern (Fig. 11) existed before this time, since these trichobothria did not exist in this pattern (only V_1 is present). Based on this observation it seems clear that the 'proto-DA' pattern occurred well before the minimum 55 Ma time-line discussed above, but after the archaeobuthids, 125 Ma. Based on this bracketing of time-lines, we suspect significant activity involving trichobothria derivation occurred within the 110-125 Ma period, in the middle of the Lower Cretaceous.

Formal statement of types D and P orthobothriotaxy

We have decided (albeit, somewhat arbitrarily) that we will establish formal orthobothriotaxic patterns under two situations: unique patterns existing in Recent scorpions, which we have four, and the oldest fossil pattern, in this case, as found in the palaeopisthacanthids. 'Intermediate' patterns, such as that exhibited in *Archaeobuthus*, is assigned a pattern identifier, F1, representative of the 'first' fossil orthobothriotaxic intermediate pattern. We suspect as more fossils are discovered and analyzed that other patterns will be uncovered. In the future a consolidation of these fossil patterns may merit other 'formal' pattern types.

Fig. 13 presents Type D orthobothriotaxy representative of Recent scorpion family Pseudochactidae. The diagrammatic pedipalp pattern is from an actual specimen of *P. ovchinnikovi*. The individual trichobothria designations are based on homologies established in this paper, which in general, are the same as those originally proposed by Gromov (1998).

Fig 14 presents Type P orthobothriotaxy representative of the fossil scorpion family Palaeopisthacanthidae. This diagrammatic pattern is based on the sketch-like illustrations provided by both Kjellesvig-Waering (1986,

Text-Figs. 103-105) and Jeram (1994, Text-Figs. 2, 4 and 7). These segment outlines are rendered without detail due to the fragmentary and composite nature of their construction. In general it appears the palaeopisthacanthids had fairly elongated fingers with a 'squared-off' chelal palm on the proximal aspect. As established in this study, the trichobothria for the femur and patella are based on a composite of palaeopisthacanthid species and the chela is based entirely on that described and illustrated by Jeram (Text-Fig. 2) for *Palaeopisthacanthus schucherti*. Individual trichobothria designations are based on the homologies established in this paper, again in many cases, the same as those originally established by Jeram.

Phylogenetic observations

The analysis presented above, based solely on fundamental orthobothriotaxic patterns for the pedipalp (Fig. 8), implies that *Archaeobuthus* is the plesiomorphic sister group to all Recent scorpions, all of them, however, combining inside the palaeopisthacanthids, the most primitive member of our ingroup. This overall result is not surprising, one would expect that the Upper Carboniferous scorpions would be the most primitive scorpion group with respect to the existence of trichobothria, where it exhibited the least numbers. Also, *Archaeobuthus* combining between the ancient palaeopisthacanthids and Recent scorpions is not surprising, it having the second lowest number of trichobothria and existing in the Lower Cretaceous.

Within the Recent scorpions are two well-formed subclades showing strong support, the buthids + pseudochactids (i.e., Types A and D) and the chaerilids + 'other scorpions' (i.e., Types B and C). All of these four fundamental clades are endorsed by significant bootstrap/jackknife support.

Pseudochactas: Of particular interest in this paper is the phylogenetic placement of the recently described

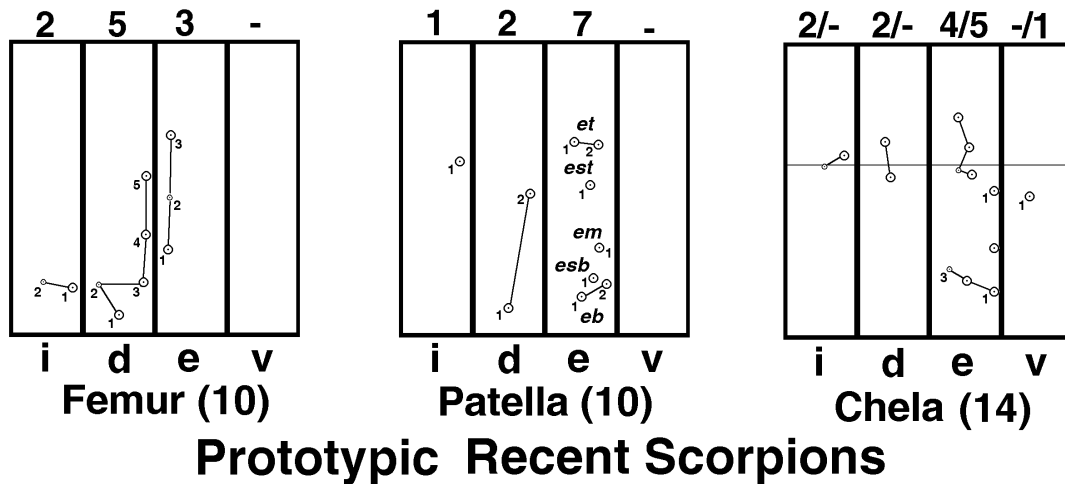
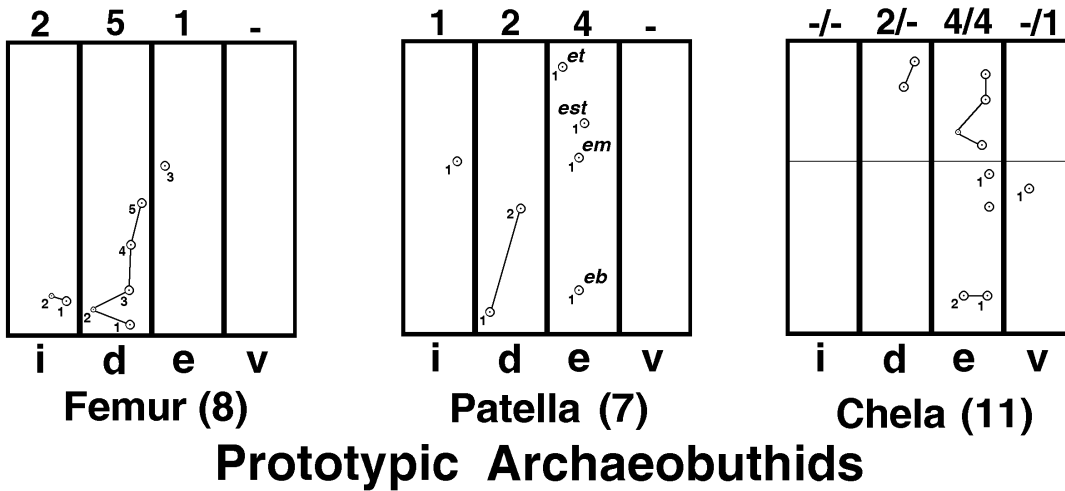
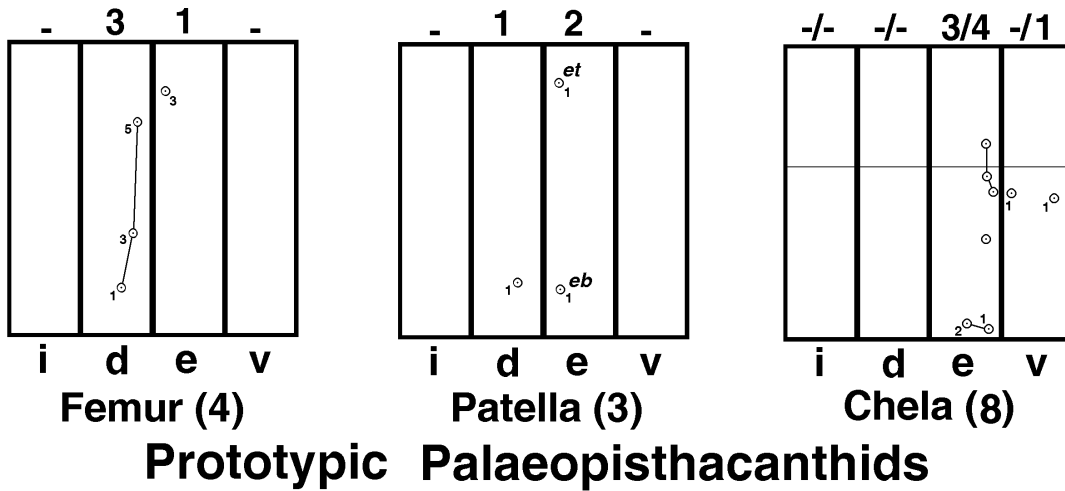


Figure 10: Hypothesized ancestral trichobothria patterns for prototypic palaeopisthacanthids, archaeobuthids and Recent scorpions. Diagrams split into fixed finger area, upper region, and palm area, lower region. Number of trichobothria per surface indicated on top of diagrams (fixed finger/palm). *i* = internal, *d* = dorsal, *e* = external and *v* = ventral surfaces.

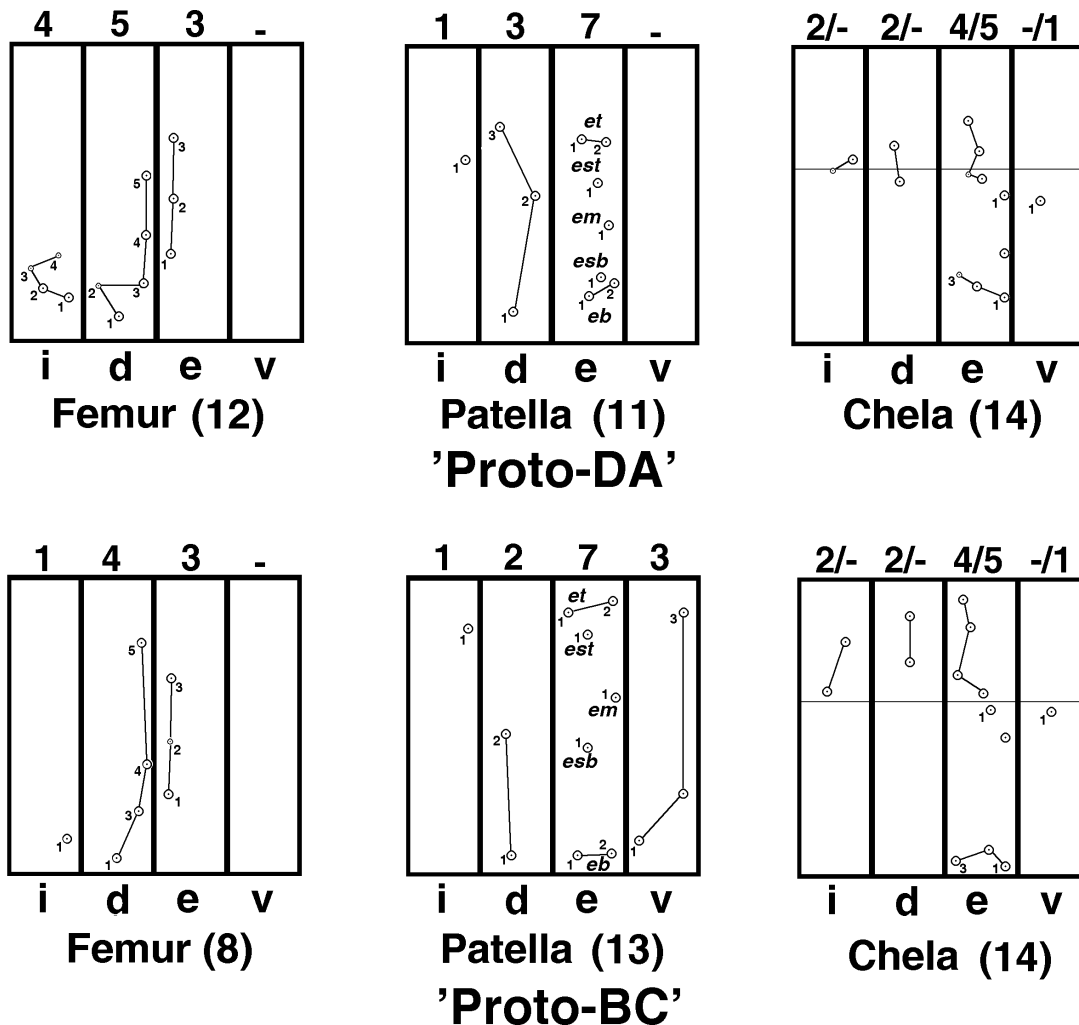
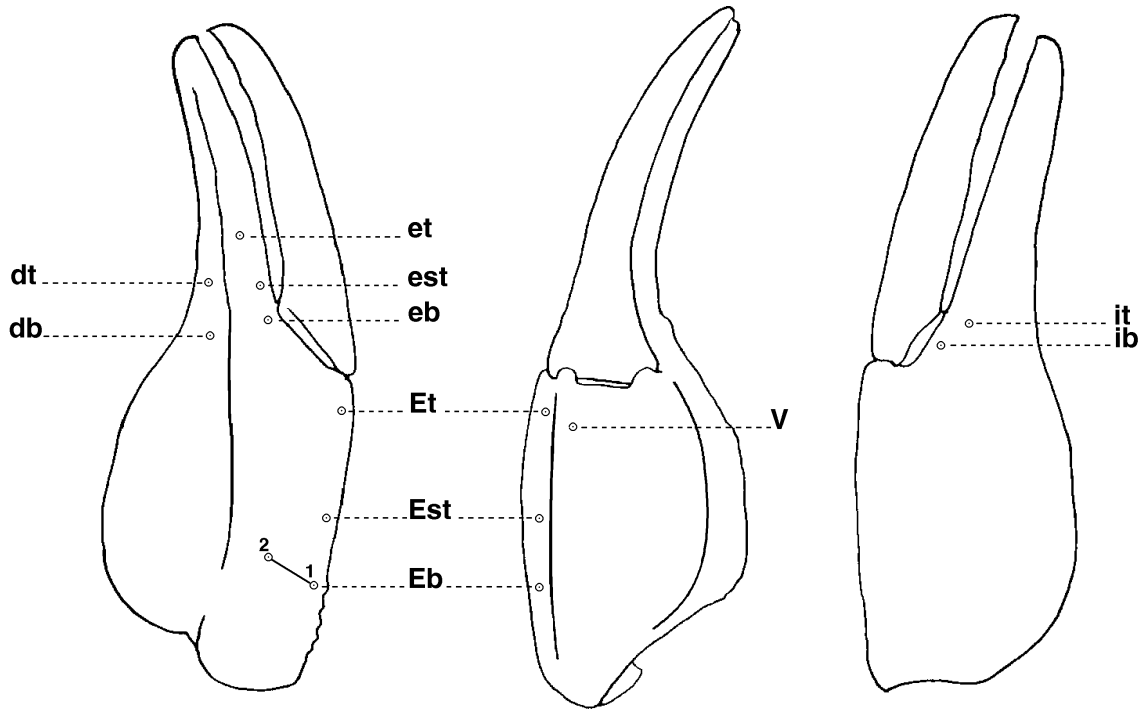


Figure 11: Hypothesized ancestral trichobothria patterns for prototypic Recent scorpion subclades 'D + A' and 'B + C'. Diagrams split into fixed finger area, upper region, and palm area, lower region. Number of trichobothria per surface indicated on top of diagrams (fixed finger/palm). *i* = internal, *d* = dorsal, *e* = external and *v* = ventral surfaces.

Recent scorpion *Pseudochactas* Gromov, 1998. As discussed elsewhere in this paper, Lourenço (2000) placed Pseudochactidae in the superfamily Chaeriloidea. The constrained analysis presented in this study forcing this topology shows that this conclusion is not viable, exhibiting considerable reduction in overall support data (see Table 7). Now, this result proposed by Lourenço was combined with another result suggested by Lourenço (2001) concerning the taxonomic placement of the fossil *Archaeobuthus* which Lourenço placed in superfamily Buthoidea. The two results, both of which are not supported by the analysis presented herein, generated a significant number of extra steps in the constrained parsimony analysis of the pedipalp. Considering the bootstrap/jackknife 'consensus' support data (Table 6) across all four sets of analyses which specifically addresses the 'pseudochactid + chaerilid' and 'archaeobuthid + buthid' clades, we have 4.625% and 3.750%, respectively.

These extremely low percentages of support involved 88000 pseudoreplicates.

Based solely on orthobothriotaxic patterns, *Pseudochactas* appears to be the sister group of Recent buthids, and is somewhat derived. For example, compare the autapomorphic trichobothria derivations exhibited by *Pseudochactas* in cladogram (Fig. 8) and derivation maps shown in **Appendix B** or, compare the 'proto-DA' pattern (Fig. 11) to the homology pattern established for *Pseudochactas* (Figs. 2-4): the loss of trichobothria *Eb*₃ and *esb* and the gain of trichobothrium *ib* for the chela; the loss of *em*₁ on the patella; and the gain of trichobothria *i*₃, *i*₄ and *d*₂ on the femur. However, when considering the femoral *alpha-beta* pattern versions as defined by Vachon (1975a) for Type A, it is interesting to note that *Pseudochactas* is somewhat close to the *beta* pattern (typical of many Old World buthids), but does not comply exactly, since trichobothria *d*₃ and *d*₄ are aligned



TYPE D
PSEUDOCHACTIDAE

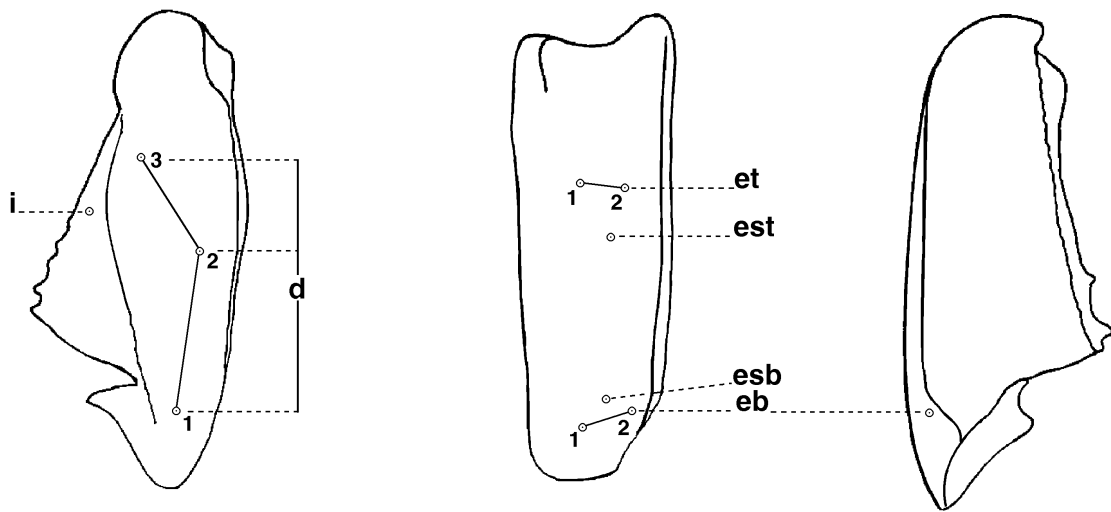
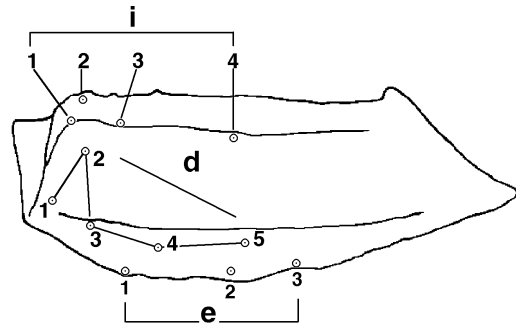
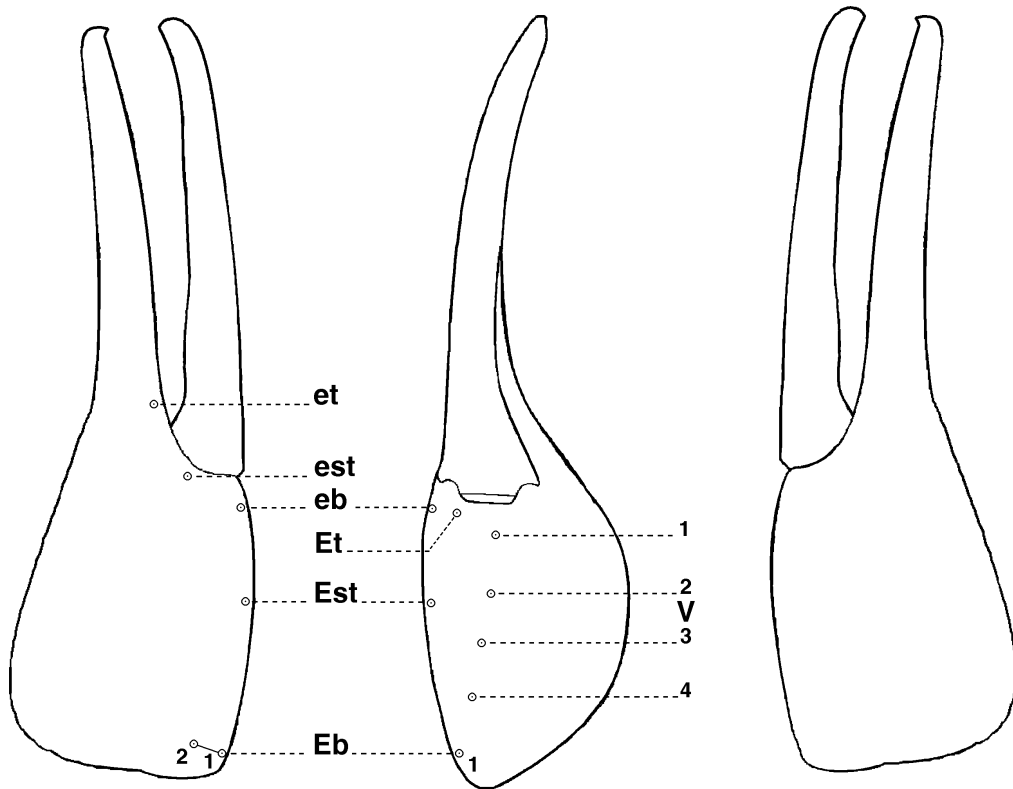


Figure 13: Scorpion orthobothriotaxy of Type D represented by scorpion family Pseudochactidae.



TYPE P
PALAEOPISTHACANTHIDAE

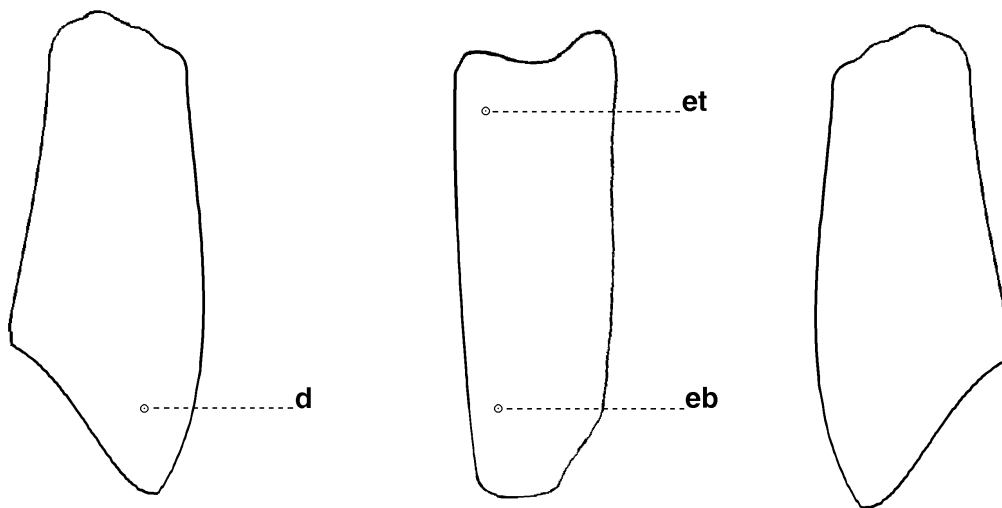
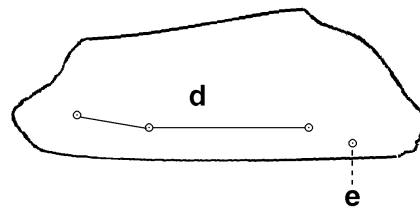


Figure 14: Proposed scorpion orthobothriotaxy of Type P represented by scorpion family Palaeopisthacanthidae.

parallel to the dorsoexternal carina, not angled as seen in typical *beta* patterns. In line with this, the archaeobuthids are also similar in this respect to *Pseudochactas*, but all three trichobothria, d_1 , d_3 and d_4 , are formed in a straight line parallel to the dorsoexternal carina (compare all three femur patterns shown in Fig. 4). Taking the *alpha-beta* pattern into consideration implies that *Pseudochactas* may be more primitive than the buthids, since based on this pattern and overall trichobothria numbers, *Pseudochactas* is intermediate between the archaeobuthids and the buthids, and therefore, possibly forming a *plesiomorphic* sister group to the buthids, thus our most primitive Recent scorpion.

In line with this relationship between *Pseudochactas* and the buthids, the chaerilids and Type C scorpions also appear to be related, being connected, in part, by the occurrence of ventral trichobothria on the patella. We suggest that *Chaerilus* is the *plesiomorphic* sister group to Type C scorpions, its patterns much closer to the 'proto-BC' pattern (Fig. 11), Type C scorpions being highly derived with respect to trichobothria gains and losses.

However, all morphology must be considered to properly determine phylogenetic placement of *Pseudochactas* within the Recent scorpions (and *Archaeobuthus* placement within the order for that matter). Therefore, we are not making taxonomic emendations at this time. As mentioned elsewhere in this paper, *Pseudochactas* also shows a close affinity to the fossil palaeopisthacanthids, based on structures such as the chelicerae, metasomal carination, leg tarsi armature, pedipalp armature, etc. This ongoing analysis, which involves a comprehensive representation of Recent scorpion genera, as well as fossil representatives such as the palaeopisthacanthids and archaeobuthids, is currently underway (Soleglad & Fet, in progress).

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References

- ARMAS, L. F., de. 1988. Situación taxonómica de *Tityus ambarensis* (Scorpiones; Buthidae) escorpión fósil de República Dominicana. *Garciana*, 11: 1-2.
- CAMPOS, D. R. B. 1986. Primeiro registro fóssil de Scorpionoidea na Chapada do Araripe (Cretáceo Inferior), Brasil. *Anais do Academia Brasileira das Ciências*, 58(1): 135-137.
- CARVALHO, M. G. P. de & W. R. LOURENÇO. 2001. A new family of fossil scorpions from the Early Cretaceous of Brazil. *Comptes Rendus des Séances de l'Académie des Sciences*, Paris, 332: 711-716.
- FARZANPAY, R. 1987 (1366). (*Knowing scorpions*). Teheran: Central University Publications, No. 312, Biology 4, 231 pp. (in Farsi, with Latin index).
- FET, V. 2000a. Family Palaeopisthacanthidae Kjellesvig-Waering, 1986. Pp. 424-425 in V. Fet et al. *Catalog of the scorpions of the world (1758-1998)*. New York, NY: New York Entomological Society.
- FET, V. 2000b. Family Pseudochactidae Gromov, 1998. Pp. 426 in V. Fet et al. *Catalog of the scorpions of the world (1758-1998)*. New York, NY: New York Entomological Society.
- FET, V. & G. LOWE. 2000. Family Buthidae. Pp. 54-286 in Fet, V., W.D.Sissom, G. Lowe & M.E. Braunwalder. *Catalog of the Scorpions of the World (1758-1998)*. New York, NY: New York Entomological Society, 690 pp.
- FET, V. & D. V. RECHKIN. 1989. Scorpion trichobothriotaxy: a principle component analysis. *Rivista del Museo Civico di Scienze Naturali "E. Caffi"*, 14: 191-206.
- FET, V., W. D. SISSOM, G. LOWE & M. E. BRAUNWALDER. 2000. *Catalog of the scorpions of the world (1758-1998)*. New York, NY: New York Entomological Society, 690 pp.
- FET, V., M. E. SOLEGLAD & M. D. BARKER. 2001. Phylogeny of the "hirsutus" group of the genus *Hadrurus* Thorell, 1876 based on morphology and mitochondrial DNA (Scorpiones: Iuridae). Pp. 139-160 in V. Fet & P. A. Selden (eds.). *Scorpions 2001. In memoriam Gary A. Polis*. Burnham Beeches, Bucks: British Arachnological Society.
- GROMOV, A. V. 1998. A new family, genus and species of scorpion (Arachnida, Scorpiones) from

- southern Central Asia. *Zoologicheskyy Zhurnal* (Moscow), 77(9): 1003–1008.
- ITTURALDE-VINENT, M. A. & R. D. E. MACPHEE. 1996. Age and paleogeographical origin of Dominican amber. *Science*, 273: 1850–1852.
- JERAM, A. J. 1989. *The Micropalaeontology of Palaeozoic Scorpions*. Ph.D. University of Manchester, UK.
- JERAM, A. J. 1994. Carboniferous Orthosterni and their relationship to living scorpions. *Palaeontology*, 37: 513–550.
- JERAM, A. J. 1998. Phylogeny, classification and evolution of Silurian and Devonian scorpions. Pp. 17–31 in P. A. Selden (ed.). *Proceedings of the 17th European colloquium of arachnology, Edinburgh 1997*. Burnham Beeches, Bucks: British Arachnological Society.
- KITCHING, I. J., P. L. FOREY, C. J. HUMPHRIES & D. M. WILLIAMS. 1998. *Cladistics (2nd Edition). The theory and practice of parsimony analysis. The Systematics Association publication No. 11*. Oxford, UK: Oxford University Press.
- KJELLESVIG-WAERING, E. N. 1986. *A restudy of the fossil Scorpionida of the world. (Palaeontographica Americana, 55)*. Organized for publication by A. S. Caster and K. E. Caster. Ithaca, NY: Paleontological Research Institution, 287 pp.
- LACROIX, J. B. 1991. Faune de France (Arachnida: Scorpionida). 6e note. 2A. Subgenus (*Polytrichobothrius*) Birula, 1917. *Arachnides*, 10: 14–25.
- LAMORAL, B. H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). *Annals of the Natal Museum*, 23(3): 497–784.
- LAMORAL, B. H. 1980. A reappraisal of the suprageneric classification of recent scorpions and their zoogeography. Pp. 439–444 in J. Gruber (ed.). *Verhandlungen. 8. Internationaler Arachnologen - Kongress Abgehalten an der Universität für Bodenkultur Wien, 7–12 Juli, 1980*. Vienna: H. Egermann.
- LEVY, G. & P. AMITAI. 1980. *Fauna Palaestina. Arachnida I. Scorpiones*. Jerusalem: The Israel Academy of Sciences and Humanities, 130 pp.
- LOURENÇO, W. R. 1996. A new genus and a new species of scorpion (Buthidae) from Iran. *Zoology in the Middle East*, 12: 93–98.
- LOURENÇO, W. R. 1997. A new genus and species of scorpion (Scorpiones, Buthidae) from Pakistan. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 12(155): 153–157.
- LOURENÇO, W. R. 1998. A new species of *Apistobuthus* Finnegan, 1932 (Scorpiones, Buthidae) from Iran. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 12(157): 237–244.
- LOURENÇO, W. R. 2000. Panbiogeographie, les familles des scorpions et leur repartition géographique. *Biogeographica* (Paris), 76: 21–39.
- LOURENÇO, W. R. 2001. A remarkable scorpion fossil from the amber of Lebanon. Implications for the phylogeny of Buthoidea. *Comptes Rendus des Séances de l'Académie des Science, Paris*, 332: 641–646.
- LOURENÇO, W. R. & D. HUBER. 2000. Two new species of scorpions (Scorpiones, Buthidae) of the genus *Paraorthochirus* Lourenço & Vachon from Oman. *Zoology in the Middle East*, 20: 137–144.
- LOURENÇO, W. R. & M. VACHON. 1995. Un nouveau genre et deux nouvelles espèces de scorpions Buthidae d'Iran. *Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie, Biologie et Écologie Animale)*, (4), 17, A, (3–4): 297–305.
- LOURENÇO, W. R. & W. WEITSCHAT. 1996. More than 120 years after its description, the enigmatic status of the genus of the Baltic amber scorpion «*Tityus eogenus*» Menge, 1869 can finally be clarified. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, 79: 183–193.
- LOURENÇO, W. R. & W. WEITSCHAT. 2000. New fossil scorpions from the Baltic amber - implications for Cenozoic biodiversity. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, 84: 247–260.
- NIXON, K. C. 1999. *Winclada (BETA) 0.9.99i*. Ithaca, NY: Published by Author.
- PAGE, R. D. M. 1998. *TreeView (win32) 1.5.2*. Glasgow, Scotland.
- PRENDINI, L. 2000. Phylogeny and classification of the superfamily Scorpionoidea Latreille 1802 (Chelicerata, Scorpiones): An exemplar approach. *Cladistics*, 16: 1–78.

- SANTIAGO-BLAY, J. A. & G. O. POINAR, Jr. 1988. A fossil scorpion *Tityus geratus* new species (Scorpiones: Buthidae) from Dominican amber. *Historical Biology*, 1: 345-354.
- SANTIAGO-BLAY, J. A. & G. O. POINAR, Jr. 1993. First scorpion (Buthidae: *Centruroides*) from Mexican amber (Lower Miocene to Upper Oligocene). *Journal of Arachnology*, 21(2): 147-151.
- SANTIAGO-BLAY, J. A., W. SCHAWALLER & G. O. POINAR, Jr. 1990. A new specimen of *Microtityus ambarensis* (Scorpiones, Buthidae), fossil from Hispaniola: evidence of taxonomic status and possible biogeographic implications. *Journal of Arachnology*, 18: 115-117.
- SANTIAGO-BLAY, J. A., V. FET, M. E. SOLEGLAD, L. M. GARIBAY ROMERO, P. R. CRAIG & S. CHEN. 2001. A Tertiary vaejovid scorpion from Mexico and another non-buthid Cretaceous scorpion from Brazil. *Geological Society of America Annual Meeting, Boston, MA, November 2001*.
- SCHAWALLER, W. 1979. Erstnachweis eines Skorpions im Dominikanischem Bernstein (Stuttgarter Bernsteinsammlung: Arachnida, Scorpionida). *Stuttgarter Beiträge zur Naturkunde*, (B), 45: 1-15.
- SCHAWALLER, W. 1981. Zwei weitere Skorpione im Dominikanischem Bernstein (Stuttgarter Bernsteinsammlung: Arachnida, Scorpionida). *Stuttgarter Beiträge zur Naturkunde*, (B), 82: 1-14.
- SELDEN, P. A. 1993. Fossil arachnids - recent advances and future prospects. *Memoirs of the Queensland Museum*, 33(2): 389-400.
- SELDEN, P. A. & A. J. JERAM. 1989. Palaeophysiology of terrestrialisation in the Chelicerata. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, 80: 303-310.
- SISSOM, W. D. 1988. *Typhlochactas mitchelli*, a new species of eyeless, montane forest litter scorpion from northeastern Oaxaca, Mexico (Chactidae, Superstitioninae, Typhlochactini). *Journal of Arachnology*, 16: 365-371.
- SISSOM, W. D. 1990. Systematics, biogeography and paleontology. Pp. 64-160 in G. A. Polis (ed.). *The biology of scorpions*. Stanford, CA: Stanford University Press.
- SOLEGLAD, M. E. 1976. The taxonomy of the genus *Hadrurus* based on chela trichobothria (Scorpionida: Vejovidae). *Journal of Arachnology*, 3: 113-134.
- SOLEGLAD, M. E. & W. D. SISSOM. 2001. Phylogeny of the family Euscorpiidae Laurie, 1896: a major revision. Pp. 25-111 in V. Fet & P. A. Selden (eds.). *Scorpions 2001. In memoriam Gary A. Polis*. Burnham Beeches, Bucks: British Arachnological Society.
- STOCKWELL, S. A. 1989. *Revision of the phylogeny and higher classification of scorpions (Chelicerata)*. Ph.D. Dissertation, University of California, Berkeley.
- SWOFFORD, D. L. 1998. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). 4.0 Beta Version. Software and Reference Manual*. Sunderland, MA: Sinauer Associates.
- VACHON, M. 1952. *Étude sur les Scorpions*. Algiers: Institut Pasteur d'Algérie, 482 pp.
- VACHON, M. 1972. Sur l'établissement d'une nomenclature trichobothriale uniforme convenant à l'ensemble des Scorpions (Arachnides) et l'existence de trois types distincts de trichobothriotaxie. *Comptes Rendus des Séances de l'Académie des Science, Paris*, (D), 275: 2001-2004.
- VACHON, M. 1974. Étude des caractères utilisés pour classer les familles et les genres de Scorpions (Arachnides). 1. La trichobothriotaxie en Arachnologie, Sigles trichobothriales et types de trichobothriotaxie chez les Scorpions. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 3(140): 857-958.
- VACHON, M. 1975a. Sur l'utilisation de la trichobothriotaxie du bras des pedipalpes des Scorpions (Arachnides) dans le classement des genres de la famille des Buthidae Simon. *Comptes Rendus des Séances de l'Académie des Science, Paris*, (D), 281(21): 1597-1599.
- VACHON, M. 1975b. Recherches sur les Scorpions appartenant déposés au Muséum d'Histoire naturelle de Genève. I. Contribution à une meilleure connaissance des espèces et des sous-espèces de Scorpions du genre "*Euscorpius*" Thorell, 1876 (Fam. des Chactidae). *Revue Suisse de Zoologie*, 82: 629-645.

Appendix A: 'Petite' Trichobothria in Recent Scorpions

In this **Appendix** we present an overview of petite trichobothria as they exist in Recent scorpions. This includes those petite trichobothria that are considered standard within an orthobothriotaxic pattern type, non-standard occurrences in orthobothriotaxic patterns, and occurrences in neobothriotaxic patterns, *accessory* petite trichobothria. Since petite trichobothria derivation plays an important role in our fundamental modeling of trichobothria existence, we believe it necessary to document cases of the gain and loss of petite trichobothria visible today in Recent scorpions. Note that this **Appendix** is not intended to be an exhaustive source for petite trichobothria documentation but does satisfy its goal of giving ample evidence of petite trichobothria gain/loss, as hypothesized in our approach to modeling trichobothria existence.

Petite trichobothria are identified by their relatively smaller size than the other full-sized trichobothria found on the scorpion. This size differential can be quantified as a difference in the diameter of the trichobothrium follicle, typically exhibiting a reduction in diameter anywhere from 10 to 45% of a normal trichobothrium. See Table A-1 for diameter ratio data of petite trichobothria for twelve scorpion genera spanning trichobothrial pattern Types C and A. Based on the very limited data presented in Table A-1, it appears that the buthids and the genus *Iurus* have the most reduced petite trichobothria. It is interesting to note that petite trichobothria have not been specifically identified as such in fossil patterns, which is probably due to a combination of the difficulty of detection because of their small size and/or their absence altogether in many fossil taxa. The smaller than usual trichobothria reported for the Carboniferous scorpion *Corniops mapesii* (Jeram, 1994), an archetypic palaeopisthacanthid species, may have indeed been petite. If so, we can propose here that the earliest trichobothria found in scorpions may have been petite in nature. In light of this possibility, Selden & Jeram (1989, p. 308) suggested 'The follicles of the earliest trichobothria may be indistinguishable from those of other setae on the same animal, the characteristic form known from Recent scorpions having developed later on'.

Orthobothriotaxic Petite Trichobothria

Normal occurrences

Petite trichobothria are formally designated in both Type A and C patterns. Therefore, their occurrences as petite trichobothria are in general consistent throughout

the species conforming to these types. This is especially true for Type C scorpions, but some variability is exhibited within Type A taxa. For Type A, three petite trichobothria are designated on the chela: Eb_3 , Esb (Et_4 in our designation) and esb ; for the patella, d_2 (d_5 is our designation); and three on the femur: d_2 , i_3 and i_4 (see Figs. 2-4). For Type C, two petite trichobothria are designated on the chela, Esb and Et_4 and one, esb_2 , is found on the patella; the femoral trichobothria are all full size. Within Type C scorpions, the petite trichobothria are frequently used as 'landmark' trichobothria in order to assist in the identification of other orthobothriotaxic trichobothria that are obscured by major neobothriotaxic patterns (Soleglad & Sissom, 2001). They are also used to establish homologous designations within unusual patterns that exhibit significant dislocation of trichobothria. Petite trichobothria have not been reported for scorpions conforming to Types B and D, but this accounts for only two genera.

Within Type C the Old World iurids, subfamily Iurinae, have five *additional* petite trichobothria occurring on the chela and patella as follows: chela, Est , esb and V_2 ; and patella, eb_2 and et_2 . These petite trichobothria are found in both Iurinae genera, *Iurus* and *Calchas*, two very diverse species (see Vachon, 1974, Figs. 212-219). See Table A-2 for diameter ratio data for these five petite trichobothria. Since the iurids are proving to be basal in Recent scorpions (Soleglad & Sissom, 2001), these curious petite trichobothria might represent an early form of the Type C pattern. If this is the case, then we have an example of petite trichobothria that have not yet become full trichobothria as seen in other Type C scorpions. On the other hand, these orthobothriotaxic trichobothria may be autapomorphic to Iurinae, and therefore we have an example of full orthobothriotaxic trichobothria becoming petite. In either case, we consider these petite trichobothria in Iurinae phylogenetically significant and investigate their origin in the companion paper discussed elsewhere (Soleglad & Fet, in progress).

Abnormal occurrences

In the remarkable small litter scorpion *Typhlochactas mitchelli* Sissom (Sissom, 1988) (Superstitionidae), no less than five additional petite orthobothriotaxic trichobothria are present: for the chela we find Db , Et_5 and esb ; and for the patella, db and dt . Whereas we consider the additional petite trichobothria present in the Old World iurids important in a phylogenetic sense (found in two diverse genera), we consider the petite condition exhibited in *T. mitchelli* to be localized to this species and probably due, in part, to the species incredibly small size (adults total length 8.49 – 8.99 mm.). In line with this suspicion, other unusual character loss and/or reduction is also found in this species: loss of some denticles on both the fixed and movable fingers of the chelicerae and

| | Type C | |
|--|---------------|--------------|
| | Et_4 / Et_5 | Esb / Eb_1 |
| <i>Vaejovis eusthenura</i> (Wood) | 0.727 | 0.667 |
| <i>Smeringurus aridus</i> (Soleglad) | 0.700 | 0.750 |
| <i>Megacormus gertschi</i> Diaz Nájera | 0.833 | 0.900 |
| <i>Brotheas granulatus</i> Simon | 0.778 | 0.667 |
| <i>Diplocentrus ochoterenai</i> Hoffmann | 0.800 | 0.786 |
| <i>Heterometrus petersii</i> (Thorell) | 0.818 | 0.864 |
| <i>Hadrurus concolor</i> Stahnke | 0.722 | 0.750 |
| <i>Iurus dufourei</i> (Brullé) | 0.706 | 0.600 |
| <i>Superstitionia donensis</i> Stahnke | 0.714 | 0.767 |

| | Type A | |
|---------------------------------------|------------|---------------|
| | esb / eb | Eb_3 / Eb_2 |
| <i>Centruroides exilicauda</i> (Wood) | 0.667 | 0.667 |
| <i>Isometrus maculatus</i> (DeGeer) | 0.714 | 0.667 |
| <i>Androctonus bicolor</i> Ehrenberg | 0.750 | 0.778 |

Table A-1: Morphometric ratios based on diameter of chelal trichobothrium follicle for Types C and A genera: petite trichobothrium compared to full-sized trichobothrium. Petite trichobothrium is *numerator* in each ratio.

loss of basal inner accessory denticles on the chelal fingers.

- *Apistobuthus*: patella, d_2 (our d_3)
- *Razianus*: patella, d_2 (our d_3)

Neobothriotaxic Petite Trichobothria ('accessory')

Petite trichobothria are also found in neobothriotaxic patterns, both *additive* and *subtractive* (i.e., *majorante* and *minorante sensu* Vachon, 1974). Vachon identified both types of neobothriotaxy for Type A scorpions, in particular, the subtractive form is interesting with respect to petite trichobothria since it involves a loss. Based on a survey of buthid genera descriptions since Vachon's large work on Northern African scorpions (Vachon, 1952) we list the following buthid genera that were attributed with the loss of petite trichobothria:

- *Lissothus*: chela, esb ; femur, d_2
- *Karasbergia*: chela, Eb_3 ; femur, d_2 ; patella, d_2 (our d_3)
- *Microbuthus*: chela, Esb (our Et_4), Eb_3 ; femur, d_2
- *Orthochirus*: femur, d_2
- *Zabius*: femur, d_2
- *Pakistanorthochirus*: femur, d_2
- *Baloorthochirus*: femur, d_2^*
- *Orthochiroides*: femur, d_2^*
- *Parabuthus*: patella, d_2 (our d_3)

Trichobothria asterisked (*) appear to be an issue of misidentification: the femoral d_2 is lost but an additional internal trichobothrium is added. Due to the close proximity of d_2 to the dorsointernal carina of the femur, the migration of d_2 to the internal surface appears to be the most prudent interpretation. It should be noted that species of *Microbuthus* and *Orthochirus* are small-sized, so the combination of scorpion size and petitness of the trichobothria may also be a factor in the loss of petite trichobothria, especially when variability in the loss is exhibited (as suggested above for *T. mitchelli*). For example, in *Karasbergia*, Lamoral (1979) reported that Eb_3 was quite small or was lost altogether, thus exhibiting variability in this character (Vachon (1974) reported it lost). Variability of this loss within a species and/or genus is also indicated in the genera *Orthochirus*, *Parabuthus* and *Apistobuthus* (the latter personally reported to us by Graeme Lowe). The impact of unreported variability in petite trichobothria loss combined with potential misidentification of individual trichobothrium is further exasperated when these same trichobothria are used as key diagnostic characters in the definition of new genera. However, other cases of subtractive neobothriotaxy may be phylogenetically significant, especially if the loss is constant across the species and/or genus involved. When conducting existence analysis as in

| | Chela, Fixed Finger | | | | | |
|-----------------------------------|---------------------|------------|-----------|-------------|-------------|-----------|
| | ia_1/ib | ia_2/ib | ia_3/ib | ia_4/ib | ia_5/ib | ia_6/ib |
| <i>Hadrurus arizonensis</i> Ewing | 0.910 | 0.727 | 0.636 | 0.545 | 0.545 | 0.545 |
| <i>Hadrurus arizonensis</i> Ewing | 1.000 | 0.938 | 0.875 | 0.813 | 0.875 | 0.687 |
| <i>Hadrurus pinteri</i> Stahnke | 1.000 | 1.000 | 1.000 | 0.900 | 0.700 | 0.600 |
| <i>Hadrurus hirsutus</i> (Wood) | 1.000 | 0.889 | 0.844 | 0.778 | - | - |
| <i>Hadrurus obscurus</i> Williams | 0.889 | 0.889 | 0.722 | - | - | - |
| <i>Hadrurus spadix</i> Stahnke | 1.000 | 0.733 | - | - | - | - |
| | Chela | | | Patella | | |
| | esb/eb | Est/Et_1 | V_2/V_1 | et_2/et_1 | eb_2/eb_1 | |
| <i>Iurus dufourei</i> (Brullé) | 0.684 | 0.600 | 0.684 | 0.550 | 0.778 | |

Table A-2: Morphometric ratios based on diameter of trichobothrium follicle for genera *Hadrurus* and *Iurus*: petite trichobothrium compared to full sized trichobothrium. Petite trichobothrium is numerator in each ratio. *ia* = internal accessory.

this research the absence of an individual trichobothrium can be interpreted two ways: (1) the trichobothrium has been lost, and (2) the trichobothrium never existed on this taxon. The latter case is, of course, very important because it may imply a more basal taxon. The first case would imply a more derived taxon.

Petite trichobothria in Type C neobothriotic patterns are also present. Of particular interest is the occurrence of petite internal accessory trichobothria found in some iurid species of *Hadrurus*, a rare and unusual location for accessory trichobothria. These accessory trichobothria, exhibiting numbers as high as seven in some cases (*H. arizonensis* Ewing), become progressively more petite as their location continues from the *ib/it* trichobothrium pair to the base of the finger/palm juncture. For the more terminal internal accessory trichobothria, the trichobothria may be full sized. On some specimens, the most proximal trichobothria are so small they are quite difficult to discern. Based on significant statistical data collected on *Hadrurus* (Soleglad, 1976; Fet *et al.*, 2001), it can be strongly suggested that accessory trichobothria in the internal series are being lost during species dispersal (as indicated by lower counts at all geographical range extremities). These losses occur at the most proximal aspect of the series, the smallest petite trichobothria. Other species of *Hadrurus* that have a smaller number of internal accessory trichobothria, the petiteness of proximal trichobothria in the series is not as pronounced (e.g., *H. obscurus* Williams). See Table A-2 for diameter ratio data illustrating the unusual progressive diameter decrease in the genus *Hadrurus*.

The euscorpoid species *Euscorpoid italicus* (Herbst) has one of the more complicated trichobothria patterns in all scorpions. This interesting and complex pattern includes an external patellar series peculiar only to this species, esb_a (see Vachon, 1975b, Fig. 21, for a formal

definition of this series). This series contains one or two additional petite accessory trichobothria in some populations of *E. italicus* (see Lacroix, 1991, Figs. 127, 129 and 131 illustrating specimens from Turkey). Yet other populations do not have petite accessory trichobothria in the esb_a series. In general, the petite accessory trichobothria occur only in those populations exhibiting larger numbers of accessory trichobothria in this series. Due to the variability of accessory trichobothria in this series, we consider this an example of the instability of petite accessory trichobothria as that discussed above for *Hadrurus*. Whether this loss is derived due to species dispersal, as suggested for the genus *Hadrurus*, remains to be seen.

Appendix B Trichobothria Derivation Maps

In this Appendix we present orthobothriotaxic derivation maps (Figs. B-1 – B-3) of each pedipalp segment based on the resulting cladogram of the pedipalp (Fig. 8). For each segment these maps show all derivations of each trichobothrium as they relate to a particular cladogram node, five internal and six terminal nodes, respectively. Each map is segregated into three regions: (1) three fossil based nodes, those representing fundamental prototypic clades of fossils and Recent scorpions; (2) two ancestral nodes that partition the Recent scorpions; and (3) the six terminal nodes (i.e., the taxa). Although all derivation maps are based on ACCTRAN character optimization as shown in Fig. 8, Figs. B-1 – B-3 indicate all unambiguous derivations; derivations that are compliant to both ACCTRAN and DELTRAN (i.e., delayed optimization) but are ambiguous; and those derivations that are only compliant with ACCTRAN. It is noteworthy to point out here that out of 62 derivation maps, only six are ambiguous.

We now present several examples which illustrate how to interpret these maps, each one presenting interesting derivations. Chela (Fig. B-1): Trichobothrium Eb_3 first occurs in the prototypic Recent scorpion node as a petite trichobothrium. It then becomes a full trichobothrium at node B+C and then is lost in Type D (i.e., *Pseudochactas*) - three separate derivations, exhibiting some homoplasy. In contrast, trichobothria Eb_1 and Eb_2 occur at the prototypic palaeopisthacanthid node, the earliest known occurrence of trichobothria, and are present from that time on for *all* known taxa, a single derivation per trichobothrium, no homoplasy. We can conclude from these derivations that Eb_3 is a pivotal trichobothrium in the phylogeny of Recent scorpions. For example, analysis considering the chela alone (Fig. 5), *Pseudochactas* does not lose Eb_3 , the homoplasy occurring on other nodes. Consider the derivation of chelal fixed finger dorsal trichobothria db , dsb , dst and dt . We see that db and dt first occur at the ‘proto-F1’ node and are present on all taxa from this point (i.e., only absent in the ancient palaeopisthacanthids), and, in contrast, the other two dorsal trichobothria, dsb and dst , derived somewhat recently, on Type C scorpions. Consider internal trichobothria on the chela, ib and it , which did not exist on our fossil representatives, first appearing on the ‘proto-Recent’ node (ib petite). Trichobothrium it is present from this point on for all Recent scorpions. In contrast, trichobothrium ib goes through several derivations, petite to full on the ‘proto-BC’ and Type D nodes, and is lost on Type A. Femur (Fig. B-3): Internal trichobothrium i_2 presents an interesting set of derivations. It first occurs at the prototypic archaeobuthid node as a petite

trichobothrium. Then for *Archaeobuthus* and node A+D, i_2 becomes full in size, while it is lost in node B+C (i.e., i_2 is absent in both Types B and C scorpions). The autapomorphic occurrence of external trichobothrium e_4 is present once on the derivation map, for the chaerilids, the only scorpion exhibiting this trichobothrium. Patella (Fig. B-2): Note that for the patella, which exhibits almost no homoplasy, the derivation map is quite simple, only two trichobothria involve multiple derivations, em_1 and d_5 .

Table B-1 presents statistical data on the number of trichobothrial derivation state changes as modeled in our

| | Femur | Patella | Chela | Total |
|------------------------|-------|---------|-------|-------|
| Absent → Petite | 5 | 2 | 6 | 13 |
| Absent → Full | 8 | 22 | 25 | 55 |
| Petite → Full | 8 | - | 5 | 13 |
| Full → Petite | - | - | - | - |
| Petite → Absent | 3 | - | 3 | 6 |
| Full → Absent | 5 | 1 | - | 6 |
| Total | 29 | 25 | 39 | 93 |

Table B-1: Number of trichobothria state derivations occurring in the pedipalp analysis (Fig. 8) based on individual segments. See ‘existence’ Sankoff character definition in **Appendix C** for weight assignments for each of the six state transitions.

Sankoff character (see **Appendix C** for a definition of this character type). Out of six possible state transitions, this data shows, predictively, that in general most derivations involve trichobothria gains to one extent or another: Out of a total 93 trichobothria derivations for the pedipalp, 81 derivations involved trichobothria gains, 13 ‘absent to petite’, 55 ‘absent to full’ and 13 ‘petite to full’. Twelve derivations involved trichobothria losses, evenly split between full and petite trichobothrium losses. The femur, representing the most ‘unstable’ analysis based on the ‘more is primitive’ hypothesis, showed the most losses (eight) whereas the patella, representing the most stable analysis (i.e., the patella did not exhibit differences when analyzed separately or when combined with the other two segments) exhibited the least losses (one). Note, the derivation ‘full to petite’ was not present in the pedipalp analysis. However, it did occur in the analysis for the chela (Fig. 5), trichobothrium esb , for the Type A pattern. Petite trichobothria were involved in 32 derivations, roughly a third, showing that the parsimony process utilized the ‘petite state’ in the Sankoff character model in a significant manner.

| | Fossil Nodes | | | Recent Nodes | | Terminal Nodes | | | | | |
|---|---------------------------------|---------------------------|-------------------|--------------|----------------|----------------|----------------|--|--|---|---|
| | Prototypic Palaeopisthacanthids | Prototypic Archaeobuthids | Prototypic Recent | A+D | B+C | P | F1 | D | A | B | C |
| <i>Eb</i> ₁ | ● | | | | | | | | | | |
| <i>Eb</i> ₂ | ● | | | | | | | | | | |
| <i>Eb</i>₃ * | | | ● ² | | ● | | | L ² | | | |
| <i>Esb</i> | | | | | | | | | | | ● |
| <i>Est</i> | ● | | | | | | | | | | |
| <i>Et</i> ₁ | ● | | | | | | | | | | |
| <i>Et</i> ₂ | | | | | | | | | | | ● |
| <i>Et</i> ₃ | | | | | | | | | | | ● |
| <i>Et</i>₄ | | | | | | | | ○ | | ○ | |
| <i>Et</i> ₅ | | | | | | | | | | | ● |
| <i>Db</i> | | | | | | | | | | | ● |
| <i>Dt</i> | | | | | | | | | | | ● |
| <i>V</i> ₁ | ● | | | | | | | | | | |
| <i>V</i>₂ | | | | | | | ○ | | ○ | | ○ |
| <i>V</i>₃ | | | | | | | ○ | | | | ○ |
| <i>V</i>₄ | | | | | | | ○ | | | | ○ |
| <i>eb</i> | ● | | | | | | | | | | |
| <i>esb</i> * | | ● ¹ | | | ○ ¹ | | ○ ¹ | L | | | |
| <i>est</i> | ● | | | | | | | | | | |
| <i>et</i> | ● | | | | | | | | | | |
| <i>db</i> | | ● | | | | | | | | | |
| <i>dsb</i> | | | | | | | | | | | ● |
| <i>dst</i> | | | | | | | | | | | ● |
| <i>dt</i> | | ● | | | | | | | | | |
| <i>ib</i> * | | | ● ² | | ○ ¹ | | ○ ¹ | ○ ¹ | L ² | | |
| <i>it</i> | | | ● | | | | | | | | |

Figure B-1: Derivation map of chelal orthobothriotaxy. Refer to cladogram of pedipalp in Fig. 8 for definitions of various nodes. Large filled circle, full trichobothrium; small filled circle, petite trichobothrium; large open circle, full trichobothrium, homoplasious; small open circle, petite trichobothrium, homoplasious; 'L' inside rectangle, trichobothrium loss. P = Type P (palaeopisthacanthids), F1 = Pattern F1 (archaeobuthids), A = Type A (buthids), B = Type B (chaerilids), C = Type C (scorpionoids, etc.), D = Type D (pseudochactids). Informative trichobothria are inside *rectangle*. Derivations are based on ACCTRAN and, unless noted otherwise, all are *unambiguous* and compliant to both ACCTRAN and DELTRAN; * Trichobothrium derivation map is *ambiguous*: ¹ derivation is compliant to ACCTRAN and DELTRAN; ² derivation is compliant to ACCTRAN.

| | Fossil Nodes | | | Recent Nodes | | Terminal Nodes | | | | | |
|-------------------------|------------------------------------|------------------------------|----------------------|--------------|-----|----------------|----|---|---|---|---|
| | Prototypic Palaeopisthacanthids | Prototypic Archaeobuthids | Prototypic Recent | A+D | B+C | P | F1 | D | A | B | C |
| <i>eb</i> ₁ | ● | | | | | | | | | | |
| <i>eb</i> ₂ | | | ● | | | | | | | | |
| <i>eb</i> ₃ | | | | | | | | | | | ● |
| <i>eb</i> ₄ | | | | | | | | | | | ● |
| <i>eb</i> ₅ | | | | | | | | | | | ● |
| <i>esb</i> ₁ | | | ● | | | | | | | | |
| <i>esb</i> ₂ | | | | | | | | | | | ● |
| <i>em</i> ₁ | | ● | | | | | | □ | | | |
| <i>em</i> ₂ | | | | | | | | | | | ● |
| <i>est</i> | | ● | | | | | | | | | |
| <i>et</i> ₁ | ● | | | | | | | | | | |
| <i>et</i> ₂ | | | ● | | | | | | | | |
| <i>et</i> ₃ | | | | | | | | | | | ● |
| <i>d</i> ₁ | ● | | | | | | | | | | |
| <i>d</i> ₂ | | ● | | | | | | | | | |
| <i>d</i> ₃ | | | | ● | | | | | | | |
| <i>d</i> ₄ | | | | | | | | | ● | | |
| <i>d</i> ₅ | | | | | | | ● | | ● | | |
| <i>v</i> ₁ | | | | | ● | | | | | | |
| <i>v</i> ₂ | | | | | ● | | | | | | |
| <i>v</i> ₃ | | | | | ● | | | | | | |
| <i>i</i> ₁ | | ● | | | | | | | | | |
| <i>i</i> ₂ | | | | | | | | | | | ● |

Figure B-2: Derivation map of patellar orthobothriotaxy. Refer to cladogram of pedipalp in Fig. 8 for definitions of various nodes. See Fig. B-1 for definition of figure icons.

| Fossil Nodes | | | Recent Nodes | | Terminal Nodes | | | | | |
|---------------------------------|---------------------------|-------------------|----------------|----------------|----------------|----------------|---|----------------|----------------|---|
| Prototypic Palaeopisthacanthids | Prototypic Archaeobuthids | Prototypic Recent | A+D | B+C | P | F1 | D | A | B | C |
| i_1 | ● | | | | | | | | | |
| i_2^* | ● ² | | ⊙ ¹ | ⌈ ² | | ⊙ ¹ | | | | |
| i_3 | | | ● | | | | ● | | | |
| i_4 | | | ● | | | | ● | | | |
| d_1 | ● | | | | | | | | | |
| d_2^* | ● ² | | | ⌈ ² | | ⊙ | ⊙ | | | |
| d_3 | ● | | | | | | | | | ⌈ |
| d_4 | ● | | | | | | | | | ⌈ |
| d_5 | ● | | | | | | | | | ⌈ |
| e_1 | | ● | | | | | | | | |
| e_2^* | | ● ² | ⊙ ¹ | | | | | ⊙ ¹ | ⌈ ² | |
| e_3 | ● | | | | | | | ⌈ | ⌈ | |
| e_4 | | | | | | | | ● | | |

Figure B-3: Derivation map of femoral orthobothriotaxy. Refer to cladogram of pedipalp in Fig. 8 for definitions of various nodes. See Fig. B-1 for definition of figure icons.

Appendix C Character State Mappings

Trichobothria character state mappings presented in *interleaved* format (partial PAUP* input).

```

matrix
[ FEMUR          int  dor  ext  trich by surface]
[
  1234 12345 1234 ]
  Branchio  0000 00000 0000
  PatP      0000 20202 0020 [composite palaeo]
  Archaeob  2200 22222 0020
  PatD      2222 22222 2220
  PatA      2211 21222 2200
  PatB      2000 20222 2222
  PatC      2000 20000 2000
[
  1234 56789 0123  PAUP* char numbers]
[ PATELLA       int  dor      ext      ven
  ii dddd eeeeeeeeeeee vvv
  12 12345 bbbbsmmsttt 123
                    12345bb12t123
                    12
                    ]
  Branchio  00 00000 000000000000 000
  PatP      00 20000 2000000000200 000 [composite palaeo]
  Archaeob  20 22002 2000000202200 000
  PatD      20 22200 2200020002220 000
  PatA      20 22221 2200020202220 000
  PatB      22 22000 2200020202220 222
  PatC      20 22000 2222221222222 222
[
  12 34567 8901234567890 123  PAUP* char numbers]
[ CHELA        int  dor      ext      ven
  ii dddd DD eeee EEEEEEEEEEE VVVV
  bt bsst bt bsst bbssttttt 1234
                    bt      bt 123bt12345
                    ]
  Branchio  00 0000 00 0000 0000000000 0000
  PatP      00 0000 00 2022 2200220000 2222
  Archaeob  00 2002 00 2222 2200220000 2000
  PatD      22 2002 00 2022 2200220000 2000
  PatA      02 2002 00 2122 2210220010 2200
  PatB      22 2002 00 2222 2220220000 2000
  PatC      22 2222 22 2222 2221222212 2222
[
  12 3456 78 9012 3456789012 3456  PAUP* char numbers]
;
outgroup Branchio [all-zero Outgroup] ;
begin assumptions ;
[EXISTENCE --- Trichobothria: absent-petite-full]
usertype existence stepmatrix = 3 012
          [Abs]   [Petite]  [Full]
[Abs]      0       1        2
[Petite]   1       0        1
[Full]     2       1        0
;
endblock ;
ctype existence: all ;

```