

Evolution of Scorpion Trichobothriotaxy: A Cladistic Approach

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TNR-12B

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TNR-10

Summary

Level-1, TNR-12B

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 Early Cretaceous archaeobuthids. An overview of all fossil scorpion material where trichobothria are reported is provided. The approach used in this analysis is to model the existence of individual trichobothrium, adding 'half size' and 'full size' as incremental stages of a trichobothrium's development. Of particular interest is the phylogenetic placement of *Pseudochactas* within Recent scorpions, 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, binding 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 our earliest fundamental trichobothrial pattern, and the pseudochactids, Type D, the fourth fundamental pattern for Recent scorpions.

TNR-10, para = 0.9

Introduction

Level-1, TNR-12B

The goal of this study is to investigate the evolution of scorpion trichobothria patterns using cladistic techniques. Our secondary goal, in support of a companion paper (Soleglad and Fet, in progress), is to determine the phylogenetic placement of the recently described and very unique scorpion *Pseudochactas ovchinnikovi* Gromov, 1998. This goal is further enhanced by two events: 1) the recent analysis of fossil scorpion trichobothria patterns conducted by Jeram (1994) and Lourenco (2001); and 2) the obtainment of *Pseudochactas ovchinnikovi* for study. With Jeram and Lourenco'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 charac-

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Document body, Dual Columns: 0.15" space, TNR-10

Automatic Hyphenation

ters that are combined with other character analysis 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 certainly a basal group 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 same.

Use of Trichobothria in

Level-2, TNR-11BI

Vachon, in his monumental treatise on the formal presentation of scorpion trichobothrial patterns (1972, 1974), established the importance of trichobothria in upper level systematics by showing very significant consistency across large numbers of genera

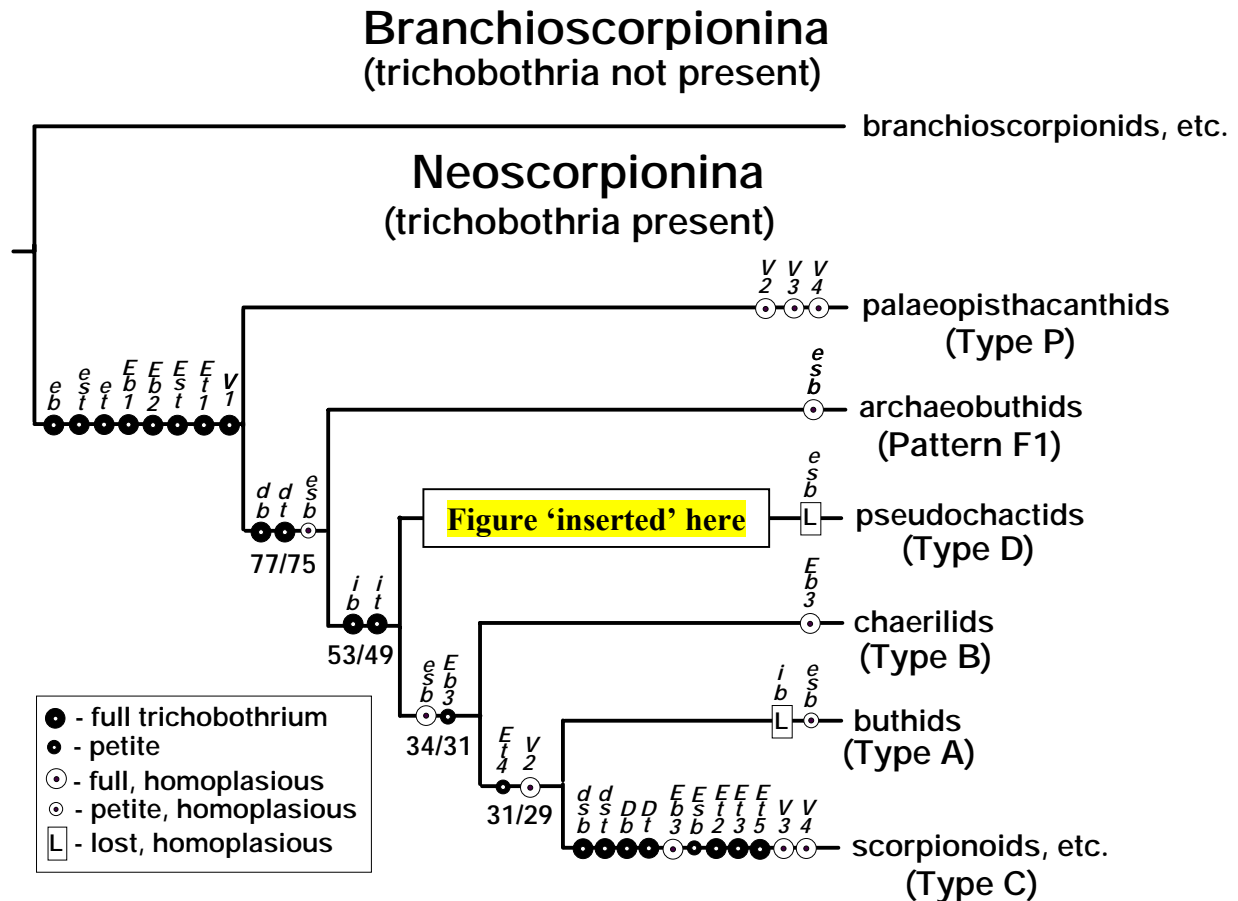


Fig. 5: Cladogram showing the distribution of trichobothria in Branchioscorpionina and Neoscorpionina. Bootstrap/jackknife support values indicated below each branch, presented as **Caption Text, TNR-9, para = 0.9**. 1000 pseudoreplicates each.

in Type A, which is predictable, since it is present in the other three Recent scorpion types.

Patella: Fig. 6 **Level-3, TNR-10BI** am of analysis of the patella for an six character pattern 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 deri-

vation 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 show **Level-3, TNR-10BI** the analysis of the femur for an six character 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 is not single stemmed, but instead, Type C

Topology	Steps (extra)	CI	RI	Table Headings, TNR-11B	
					reduction (%)
Lourenço, 1	118 (+20)	0.5508	0.4111	-22.907	17/35.1/14.2
Row Labels, TNR-11B	118 (+20)	0.5508	0.4111	-22.907	17/35.1/14.2
Lourenço, 2	120 (+22)	0.5417	0.3889	-22.507	18.3/38.6/15.7
Alternative	10	Data, TNR-10, para = 0.6		5.757	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. Const alternative top from the pedipalp ('total' analysis). See Fig. 8 for original topology derived from in table. Caption Label, TNR-10B Caption Text, TNR-9, para = 0.9

trichobothria, eight femoral, seven on the patella, and 11 on the chela; for prototypic Recent scorpions, we add in the eight trichobothria distribute 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 provide differences from the terminal nodes, in most cases a more primitive pattern; that is, a pattern with either less 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 Eb_3 ; the patella, *Pseudochactas* loses em_1 ; and the femur, the buthids loses e_3 , and Type C scorpions, with a lose of five trichobothria, d_3-d_5 and e_2-e_3 . 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 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 ar-

chetypic 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 evolutionary time-line with Level-3, TNR-10BI

an evolutionary time-line with orthobothria 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 buthids, is found in its entirety in the Old World at least 55 million years ago, in the Eocene (based on the 'palaeobuthids'). 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 55 Ma. New World buthid patterns complying to typical Type A existed at least 15-20

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References body, Dual Columns: 0.15" space, TNR-10

Appendix A:

‘Petite’ Trichobothria

Appendix Title, TNR-14B

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 a 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 trichobothria existence, we 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.

Appendix body, Dual Columns: 0.15” space, TNR-10

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 *butids* 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”.

Orthobothriota

Level-1, TNR-12B

Normal occurrence

Level-2, TNR-11BI

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 trichobothria. 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 to 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 occurrence

Level-2, TNR-11BI

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