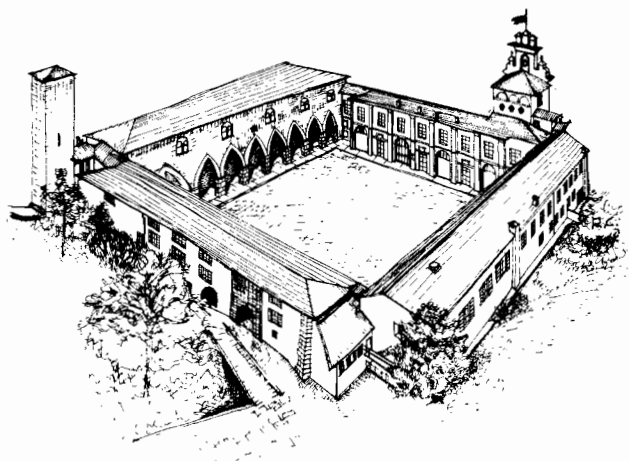ESTRATTO

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SCORPION TRICHOBOTHRIOTAXY:

A PRINCIPAL COMPONENT ANALYSIS

RIASSUNTO:
Si analizzano i pattern tricobotriali di numerosi generi, sottogeneri, specie e sottospecie di scorpioni, appartenenti a tutte le famiglie conosciute. Attraverso un'analisi multifattoriale si riconoscono e si descrivono quattro principali tendenze evolutive. La prima, desumibile dalla variazione della tricobotriotassia femorale, è la divergenza ancestrale in tre tipi tricobotriotassici, A, B e C, già riconosciuti dallo studio di Vachon (1974). Dall'analisi emergono inoltre le tendenze alla politrichia, sia di tipo saltatorio, sia di tipo graduale, all'interno del tipo C. Infine si evidenzia la riduzione di tricobotri nei pattern est, esb e Eb in alcuni generi di Buthidae, (tricobotriotassia di tipo A). La più importante tendenza evolutiva riconoscibile negli scorpioni attuali è la politrichia generale, evidente sopratutto negli "euscorpiidae", che raccolgono le sottofamiglie Euscorpiinae + Megacorminae + Scorpiopsinae, a conferma della loro già riconosciuta prossimità filogenetica.

SUMMARY:
The variation of trichobothrial patterns in scorpions is described by principal component analysis (PCA). Four principal components describe the following independent trends of variaiton: the ancestral divergence into three "types" of trichobothriotaxy (A, B and C) of Vachon (1974); saltatoric polytrichy in "type C"; gradual polytrichy in "type C"; reduction in "type A". The most important trend of polymorphism in modern scorpions is gradual polytrichy, especially significant in the "euscorpiid" complex (Euscorpiinae + Scorpiopsinae + Megacorminae).

РЕЗЮМЕ
Путем анализа главных компонентов изучалась трихоботриотаксия отряда скорпионов (Chelicerata: Scorpionida). Обнаружены следующие, статистически независимые направления полиморфизма: анцестральное расхождение на три основные "типа" А, В и С; сальтаторная (внезапная) политрихия в пределах типа С; постепенная политрихия в пределах типа С; редукция в пределах типа А. Наиболее важным механизмом полиморфизма среди современных скорпионов является постепенная политрихия "эускорпиид" (Euscorpiinae + Scorpiopsinae + Megacorminae).

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INTRODUCTION: The trichobothria are sensory bristles present in all recent scorpions (Chelicerata, Scorpiones) and responsible for mechanoreceptory functions (Reissland and Gorner 1985). Trichobothria in scorpions are found only on three segments of pedipalp: femur, tibia and manus (Fig. 1). The patterns (number and mutual position) of trichobothria are the basic criteria in scorpion taxonomy (genus/family level) (Vachon 1974; Sissom 1990).
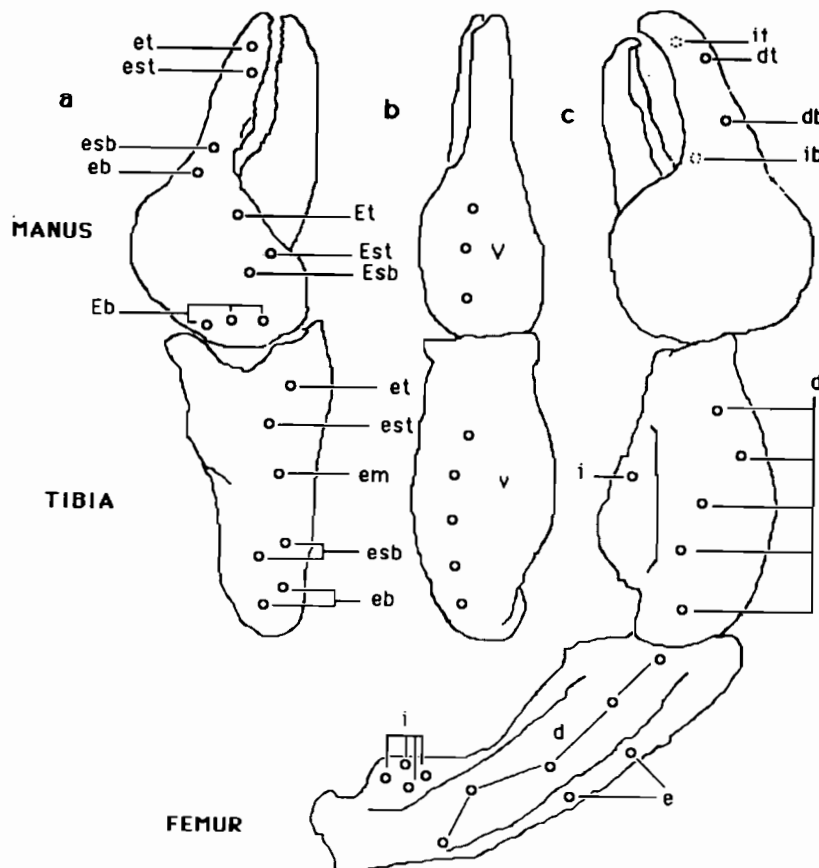
Fig. 1 A generalized trichobothrial pattern of a scorpion:
a-external view, b-ventral view, c-dorsal view.

Vachon (1972, 1974), studied 97 scorpion genera and developed the system of trichobothrial criteria. He grouped all scorpion taxa along three "types of trichobothriotaxy" (A, B and C). Taxonomic level of these groups is close to the superfamily. Lamoral (1980) refers to these groups as to "lines" of "buthoids", "chaeriloids" and "diplocentroids". The real status of superfamilies remains very uncertain: Kjellesvig-Waering (1986) consi-

dered all recent families as belonging to one superfamily, as opposed to the numerous superfamilies of fossil scorpions.

Here we use following names: buthoids ("type A" of Vachon, family Buthidae), chaeriloids ("type B", family Chaerilidae) and scorpionoids* ("type C", including families: Bothriuridae, Chactidae, Diplocentridae, Ischnuridae, Iuridae, Scorpionidae and Vaejovidae).

Sissom (1990) notes that, in trichobothriotaxy, "the variability in number and pattern is great... and this variability is not well understood for many taxa". The objective of this study was to demonstrate some possible phylogenetic trends within the extant Scorpionida. Several basic patterns of trichobothrial polymorphism are observed in scorpions. Independent trends in these patterns can be revealed by multivariate statistical analysis.

MATERIAL AND METHODS: The initial matrix (Tab. 1) included 72 rows and 38 columns. Each row corresponds to a certain scorpion taxon (genus, subgenus, species and, in some cases, subspecies), and each column contains the number of trichobothria in a certain "territory" or "series" of trichobothria (Vachon, 1974) (Fig. 1).

The last paper was the general source of information on trichobothrial patterns. Some other papers described additional combinations (Armas 1977; Bonacina 1980; Fet 1985,1987; Francke 1981; Francke and Soleglad 1981; Gonzales-Sponga 1980, Lamoral 1979; Levy and Amitai 1980; 1978, 1980, 1981; Vachon and Jaques 1977; Valle 1975). Original data on *Euscorpius* (V. Fet) were also included.

Column: 27 columns were initially selected, and later 11 pooled characters were added (defined as sums of trichobothria in particular territories and/or series).

Rows: Vachon (1974) demonstrated that the majority of scorpion genera in his "types" A and C are "orthobothriotaxic", i.e. patterns of trichobothria are not only constant within the certain genus but also identical for all "orthobothriotaxic" genera within the family or even several families (in "type C"). All deviations from each "type" Vachon defined as "neobothriotaxy". "Neobothriotaxic" genera are those with accessory ("trichobothriotaxie majorante" by Vachon) or deficient ("minorante") number of trichobothria in certain "territories", compared to the "ortho"-genera. The total number of trichobothria in "neo"-genus may be more than, less than, or the same as in "ortho".

We tried to screen all possible patterns of "neobothriotaxy". As representative "ortho"-genera were chosen: *Mesobuthus* ("type A", Buthidae) and *Nebo* ("Type C, Diplocentride), respectively. "Type D" is represented only by a single genus *Chaerilus* (Chaerilidae). Us we could find, only 42 of 120 existing scorpion genera are "neobothriotaxic" (12 of "type A" and 30 of "type C"). The following 40 "neobothriotaxic" genera were included in our study: in buthoids ("type A", Buthidae): *Alayotityus, Anomalobuthus, Buthiscus, Centruroides, Karasbergia, Liobuthus, Lissothus, Microbuthus, Orthochirus*, (same pattern as *Zabius*), *Pectinibuthus, Vachonolius, Zabius;* in scorpionoids, "type C": *Brachistosternus, Centromachetes, Lisposoma* (has the same pattern as *Vaejovis*), *Timogenes, Vachonia* (Bothriuridae); *Broteas, Broteochactas, Chactopsis, Euscorpius, Megacormus, Plesiochactas, Superstitionia, Teuthraustes, Typhlochactas* (Chactidae);

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* We use the name "scorpionoids" because of taxonomic priority of the familial name Scorpionidae Latreille 1810.

Table 1

Initial Matrix: Patterns of Scorpions Trichobothria

The numbers correspond to the following groups of trichobothria by Vacon (1974): Femur (#1-4): 1 = i, 2 = d, 3 = e, 4 = i + d + e (all femoral trichobothria). Tibia (#5-10): 5 = v, 6 = d, 7 = i, 8 = et, 9 = est, 10 = em, 11 = esb, 12 = eba, 13 = eb, 14 = all tibial trichobothria. Manus: Palm (#16-23): 16 = V, 17 = i, 18 = Et, 19 = Est, 20 = Esb, 21 = Eb, 22 = all E, 23 = D; inn 24 = et, 25 = est, 26 = esb, 27 = eb, 28 = all e, 29 = dt, 30 = dst, 31 = dsb, 32 = db, 33 = all d, 34 = e + t + d. 35 = e + d + i; 36 = V + E + D; 37 = all trichobothria of the manus; 38 = the entire number of trichobothria.

GROUPS OF TRICHOBOTHRIA ("trichobothriotaxy" in bold print)

GENERA

"TYPE A":
1 Mesobuthus
2 Anomalobuthus
3 Lissothus
4 Pectinibuthus
5 Microbuthus
6 Karasbergia
7 Orthochirus
8 Centruroides
9 Buthiscus
10 Vachoniolus
11 Liobuthus
12 Aluolypus

"TYPE B":
13 Chaerilus

"TYPE C":
14 Nebo
15 Didymocentrus
16 Scorpio
17 Opisthophthalmus
18 Iludogenes
19 Heteroscorpion
20 Hadobella
21 Vachonia
22 Centromachetes
23 Brachistosternus
24 Timogenes
25 Vaejovis
26 Caraboctonus
27 Calchas
28 Paruscorpiops
29 Scorpiops (S.) (Var.1)
30 Scorpiops (S.) (Var.2)
31 S. (Alloscorpiops)
32 S. (Neoscorpiops)
33 S. (Euscorpiops)
34 Euscorpius (Polytrichobothrius)

GROUPS OF TRICHOBOTHRIA ("neobothriotaxy" in bold print)

GENERA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
35 *E. (Tetratrichobothrius)*	1	1	1	3	12	2	1	7	4	5	2	6	5	29	44	6	2	5	5	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	28	**75**
36 *E. (Euscorpius)*	1	1	1	3	5	2	1	3	4	3	2	5	4	20	25	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**54**
37 (## 36 to 62 are different	1	1	1	3	5	2	1	4	4	3	2	3	4	20	25	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**54**
38 variants within this subgenus *)	1	1	1	3	5	2	1	4	4	3	2	4	4	21	26	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**55**
39	1	1	1	3	5	2	1	5	4	3	2	4	4	22	26	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**56**
40	1	1	1	3	5	2	1	3	4	3	2	4	4	20	26	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**56**
41	1	1	1	3	6	2	1	4	4	2	2	4	4	21	27	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**55**
42	1	1	1	3	6	2	1	5	4	3	2	4	4	20	26	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**56**
43	1	1	1	3	6	2	1	5	4	3	2	4	4	21	27	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**58**
44	1	1	1	3	6	2	1	6	4	3	2	4	4	22	29	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**57**
45	1	1	1	3	7	2	1	5	4	3	2	4	4	22	28	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**58**
46	1	1	1	3	7	2	1	4	4	3	2	4	4	23	29	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**59**
47	1	1	1	3	7	2	1	4	4	3	2	4	4	23	30	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**57**
48	1	1	1	3	7	2	1	5	4	4	2	4	4	21	28	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**59**
49	1	1	1	3	7	2	1	6	4	4	2	4	4	23	31	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**60**
50	1	1	1	3	8	2	1	6	4	4	2	4	4	24	31	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**61**
51	1	1	1	3	8	2	1	6	4	4	2	4	4	24	32	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**60**
52	1	1	1	3	8	2	1	5	4	4	2	4	4	23	31	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**60**
53	1	1	1	3	8	2	1	5	4	4	2	4	4	23	31	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**62**
54	1	1	1	3	8	2	1	7	4	4	2	4	4	25	33	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**62**
55	1	1	1	3	9	2	1	6	4	4	2	4	4	24	33	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**63**
56	1	1	1	3	9	2	1	7	4	4	2	4	4	25	34	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**63**
57	1	1	1	3	9	2	1	6	4	4	2	5	4	24	34	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**63**
58	1	1	1	3	10	2	1	6	4	4	2	4	4	25	35	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**64**
59	1	1	1	3	10	2	1	7	4	4	2	4	4	25	36	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**65**
60	1	1	1	3	11	2	1	8	4	4	2	5	5	28	39	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**68**
61	1	1	1	3	13	2	1	9	4	4	2	4	5	27	40	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**69**
62	1	1	1	3	8	1	2	3	4	5	2	3	3	22	33	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**62**
63 *Megacormus gertschi*	1	1	1	3	6	1	2	2	4	3	2	3	3	19	28	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**57**
64 *M. granosus*	1	1	1	3	12	1	2	4	4	4	2	4	3	21	34	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**63**
65 *Plesiochactas dilutus*	1	1	1	3	8	1	2	4	4	4	2	4	3	21	32	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**61**
66 *P. mitchelli*	1	1	1	3	2	2	1	4	1	2	2	0	3	14	19	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**48**
67 *Superstitionia*	1	1	1	3	2	2	1	4	2	2	2	0	5	15	20	4	2	5	1	1	3	10	2	1	1	—	—	1	1	1	1	1	4	8	10	16	26	**49**
68 *Typhlochactas*	1	1	1	3	7	1	2	6	6	2	3	2	3	24	34	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**49**
69 *Brotcas lichyi*	1	1	1	3	7	1	2	6	6	2	3	2	3	22	32	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**61**
70 *Broteochactas sp.*	1	1	1	3	7	1	2	6	6	2	3	2	3	22	32	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**63**
71 *Chactopsis*	1	1	1	3	7	1	2	5	6	2	3	0	6	22	32	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	10	16	26	**61**
72 *Teuthraustes amazonicus*	1	1	1	3	7	1	2	3	6	2	3	0	5	17	25	4	2	5	1	1	3	10	2	1	1	—	—	4	1	1	1	1	4	8	13	16	29	**57**

*The trichobothrial polymorphism of subgenus *Euscorpius* (*Euscorpius*) was extensively studied, and many subspecific forms were described within its three species. The following forms correspond to the ## 36-62: ## 36-*E. germanus ssp.*; #37-*E. g. marcuzzi*; #38-*E. g. germanus*; #39-*E. mingrelicus ssp.?*, #40-*E. germanus ssp.?*, #41-44-*E. germanus alpha*; #45-*E. m. mingrelicus, E. germanus croaticus*; #46-47 *E. mingrelicus cilicensis*; #48-*E. mingrelicus ssp.?*, #49: *E. carpathicus ossae, E. c. koshevnikovi* (part), #50: *E. c. tauricus* (deviant); #51-*E. c. tauricus* (Crimea); #52- *E. c. tauricus* (part), *E. c. candiota* (Crete; part), *E. c. koshevnikovi* (part), *E. carpathicus* (part); #54, 56 and 58- *E. c. candiota* (part); #55- *E. c. tauricus* (deviant); #57- *E. c. sicanus* (Sicily); #59- *E. carpathicus* (part), *E. c. candiota* (patr); # 60- *E carpathicus* (part; Yugoslavia); # 61- *E. c. canestrinii* (Sardinia); #62- *E. c. balearicus* (Islas Baleares). Data for *Euscorpius* are compiled from Vachon (1974, 1978), Vachon and Jaques (1977), Bonacina (1980, 1983), Valle (1975) and Fet (1985, 1987, and original non-published material).

Diplocentrus (Diplocentridae); *Opisthophthalmus, Pandinus (Pandinops), Scorpio* (Scorpionidae); *Habibiella, Hadogenes, Heteroscorpion* (Ischnuridae); *Calchas* (has the same pattern as *Iurus*), *Caraboctonus, Hadrurus, Iurus* (Iuridae); *Parascorpiops, Scorpiops, Vaejovis* (Vaejovidae).

Two genera, *Dasyscorpiops* and *Anuroctonus*, were not included into this analysis because we had no information about their variability. For *Broteochactas*, two varieties of patternes were taken, those of *B. panarei* and *B.sp.* (Gonzales-Sponga 1980) (the pattern of *Broteochactas panarei* completely coincides with that of *Broteas lichyi*). The genus *Scorpiops* was divided into several groups according to Vachon's (1980) subgenera: *Alloscorpiops, Euscorpiops, Neoscorpiops* and *Scorpiops s.str.* (the last had two varieties). In *Scorpiops* and *Heteroscorpion* where number of trichobothria varied within one "territory" but no original data was available, a slot of the matrix included the average number. All the cases of so-called "migration" of a trichobothrium were considered a repression of its development in one position and emerging in the other (e.g. "migration" of the trichobothrium **d** to the position **i** in *Scorpio* was considered a repression in the series **d** and emerging of two trichobothria instead of one in **i**). For *Euscorpius* (the scorpion genus with the highest known variability of trichobothriotaxy), we included 27 varieties of trichobothrial patterns at all taxonomic levels (subgenus/species/subspecies/population).

Method: The statistical technique used in this study is a principal component analysis (PCA) operating on a correlation matrix. PCA analysis finds the principal axes of a multidimensional configuration of individual plots (taxa, species, or individuals) and determines the coordinates of each plot relative to the principal axes. The PCA output is in the form of a series of eigenvalues which are proportional to the variation accounted for by each axis, with eigenvectors which are the spatial coordinates of each plot (Blakith and Reyment 1971; Jeffers 1978; Akimov et al. 1989). We analyzed plot clustering along first four principal components (multidimensional axes) which accounted for about 80% of observed variation. The statistically significant variation accounted for by each of these axes was interpreted as an independent trend in morphological evolution.

The graph description technique was developed by V.M. Efimov (Siberian Academy of Agriculture, Novosibirsk, USSR). Computations were made by original software (applied program package STATIC vers. 2.05) developed by D.V. Rechkin on microcomputer RT-11.

All technical information can be obtained from the second author.

RESULTS AND DISCUSSION: The results of the PCA analysis (four principal components) are presented in Tables 2 and 3. All variations in trichobothria of the femur of a pedipalp are described by the principal component I, whereas variations in tibia are described only by component III, and in manus - by components II, III, and IV.

Principal component I: Differences between Vachon's "types A, B and C" are well described by the principal component I (66% of total variance). A common ancestor of all extant scorpions could be either "oligotrichous" (with hypothetic femur/tibia/manus number of pedipalp trichobothria

Charac-ters	Principal components			
	I	II	III	IV
1	0.222	0.021	0.105	0.048
2	0.22	0.029	0.117	0.179 .
3	0.196	0.005	0.095	0.163
4	0.227	0.022	0.114	0.134
5	-0.146	-0.008	0.248	0.032
6	-0.123	-0.179	0.144	0.010
7	0.219	0.080	0.031	0.081
8	-0.191	-0.144	-0.176	0.013
9	-0.144	-0.180	0.224	0.028
10	-0.165	-0.141	0.230	0.052
11	-0.014	-0.020	0.202	0.127
12	-0.122	-0.191	0.325	0.067
13	-0.187	0.071	-0.239	-0.100
14	-0.195	-0.166	0.245	0.044
15	-0.180	-0.172	0.279	0.051
16	-0.082	-0.336	0.164	-0.002
17	-0.170	-0.007	-0.173	-0.051
18	-0.231	-0.013	-0.109	-0.069
19	-0.031	0.392	0.146	-0.009
20	-0.044	0.391	0.135	0.023
21	-0.077	0.039	-0.194	0.231
22	-0.132	0.337	0.061	-0.003
23	-0.231	-0.013	-0.109	-0.069
24	0.000	0.000	0.000	0.000
25	-0.066	0.013	-0.080	0.274
26	-0.071	0.005	-0.125	0.555
27	0.000	0.000	0.000	0.000
28	-0.093	0.010	-0.148	0.622
29	0.000	0.000	0.000	0.000
30	-0.231	-0.013	-0.109	-0.069
31	-0.231	-0.013	-0.109	-0.069
32	0.000	0.000	0.000	0.000
33	-0.231	-0.013	-0.109	-0.069
34	-0.226	-0.009	-0.138	0.122
35	-0.222	-0.009	-0.163	0.062
36	-0.135	0.357	0.107	-0.003
37	-0.157	0.329	0.075	0.004
38	-0.182	0.125	0.301	0.073
D_i	0.521	0.145	0.077	0.057
C_i	0.806	0.769	0.748	0.874
N_A	18	6	14	4

where $D_i = \lambda_i / \Sigma \lambda_i$ - variance of the component i; λ_i - the eingenvalue of a component i; s_{ij} - dose of a character j in an eigenvector i; S_i - a set of most significant values in the eigenvectors i; $C_i = \Sigma s_{ij}^2$ (j belongs to S_i) - determination index for the component i; N_A - number of agglomerated characters constituting the component i (corresponds to the power of set S_i).

Tab. 2.   The significance of character dose values in building of I - IV principal components.

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Charac-ters	Principal components			
	I	II	III	IV
1 i	+	0	0	0
2 d	+	0	0	0
3 e	+	0	0	0
4 Σ femur	+	0	0	0
5 v	0	0	+	0
6 i	0	0	0	0
7 d	+	0	0	0
8 et	−	0	+	0
9 est	0	0	+	0
10 em	0	0	+	0
11 esb	0	0	+	0
12 eba	0	0	+	0
13 eb	−	0	−	0
14 Σ e	−	0	+	0
15 Σ tibia	−	0	+	0
16 V	0	+	+	0
17 i	−	0	−	0
18 Et	−	0	0	0
19 Est	0	+	0	0
20 Esb	0	+	0	0
21 Eb	0	0	−	+
22 Σ E	0	+	0	0
23 D	−	0	0	0
24 et	0	0	0	0
25 est	0	0	0	+
26 esb	0	0	0	+
27 eb	0	0	0	0
28 Σ e	0	0	0	+
29 dt	0	0	0	0
30 dst	−	0	0	0
31 dsb	−	0	0	0
32 db	0	0	0	0
33 Σ d	−	0	0	0
34 Σ e+d	−	0	0	0
35 Σ e+d+i	−	0	−	0
36 Σ V+D+E	0	+	0	0
37 Σ manus	0	+	0	0
38 Σ pedipalp	−	0	+	0

Tab. 3.   The impact of character dose values in building of I - IV principal components.
(" + " : positive impact of a character, i.e. the correlation of the character with the marked eigenvector is positive; "-" : negative   impact of a character , which is opposite to the positive impact; "0" : non-significant impact).

not more than 3/12/14 that later increased) or "polytrichous" one (with this number not less than 11/29/26 that later decreased). In fact, in femur "type C" has three trichobothria in the position i, d and e (1/1/1), "type B" has 9 (1/4/4), and "type A" has 11 (4/5/2), with variations. The same situation can be observed in tibia ("type B" has 12, "type A" 13 and "type C" 19 and more) and manus ("type B" has 14, "type A" 15, "type C" 26 and more).

Principal component analysis allows to determine that increasing or decreasing of the number of trichobothria in all surfaces of the femur and in dorsal surface of tibia are compensatory to the same trends in all other surfaces of the tibia and in positions Et, D, d and i in manus (Tab. 3). In such a case the "type C" of trichobothriotaxy can be derived only by the reduction of some trichobothria in femur and dorsal surface of tibia and increasing of their number ("polytrichy") in all other surfaces of tibia and in the mentioned positions in the manus. The opposite process did not exist.

For this reason, the common ancestor of all recent scorpions might have higher number of trichobothria in femur and dorsal surface of tibia, and the modern three "types" A, B and C can be considered as a result of various reductions. In "type C", the reduction was "compensated" by the increasing of the number of trichobothria in manus (positions Et, B, dst and dsb). No trichobothria in the last three positions are found in the "types" A and B at all; in the position Et "types" A and B have only one trichobothrium, whereas "ortho" - genera of the "type" C have five.

Thus, the polytrichy in the manus could have been an initial trend that separated the ancestor of "type" C families from the ancestors of all the other recent scorpions even before modern families were formed ("type" C is shared by at least seven modern families). The paleontological data (Kjellesvig - Waering 1986) show that as early as in Middle Carboniferous some families of scorpions were morphologically resembling the modern ones. The trichobothriotaxy of fossil scorpions is unknown but the events discussed here (the formation of A, B and C types) should have happened apparently not later than in late Cretaceous. Oligocene fossils already include modern genera (Schawaller 1979; Sissom 1990).

All the positions of trichobothria mentioned above are **not** participating in variations described by principal components II and III, i.e. are not involved in the further modifications of the sensory apparatus of pedipalps. The extreme value of correlation coefficient ($r = 1$) between the variations in described positions in manus (Et, D, dst and dsb), and without any variations within these positions, corresponds to the strictly determined development of this trichobothrial group within the "type" C. Polytrichy in Et (from 1 in "types" A and B to 5 in "type" C) can be in fact considered a polytrichy from 1 to 7 (including the appearance of two trichobothria in D).

The two general trends observed here are: polytrichy in manus and reduction in femur and dorsal surface of tibia. All positions described above were never actively modified. For "type" C, no variations in femur are known; these occur only in "type" A (buthoids), with occasionally disappearing trichobothrium d in tibia (*Alayotityus, Pectinibuthus*). The presence of this trichobothrium in "type" C, together with duplication of i in tibia as PCA results show, is independent from the other trends.

Variations in the position **d** in tibia give impact only to the component I, and variations in **i** (which are connected to **d** through the "migration" hypothesis [repression + emerging]) do not participate in any of principal components at all.

All observed independent variations described by the next three principal components (II, III and IV) refer to the modifications of Vachon's "types", i.e. represent lower taxonomic level than variation described by the component I. Figure 2 represents the clustering of "types" A, B and C as well as certain deviant genera. The axes on fig. 2 correspond to the principal components III and IV.
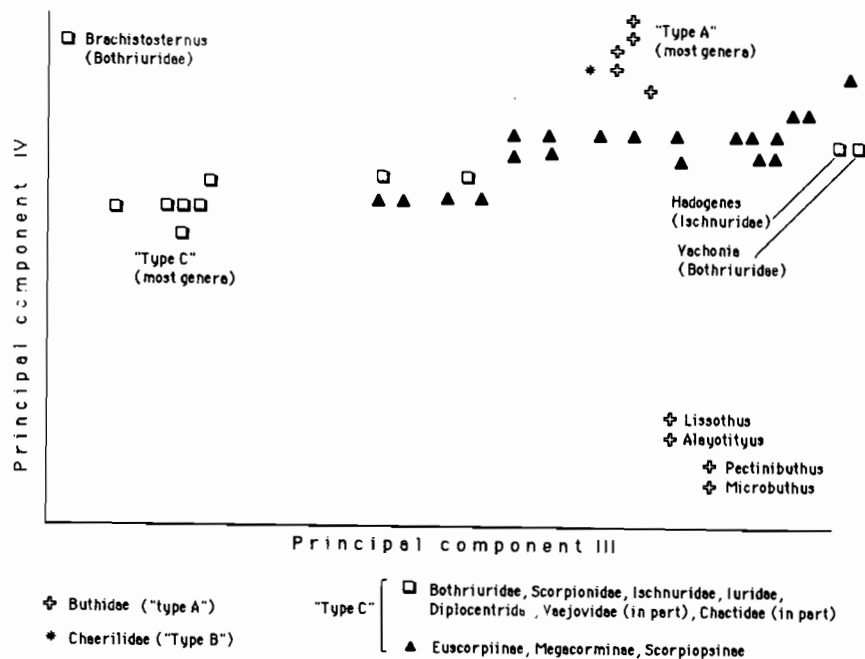
Fig. 2 Projections of the individual plots on a two-dimensional plane of principal components III and IV.

Principal components II and IV: The variation described by these components involves only positive impact in the variation of positions in manus (component II: positions **V, Est** and **Esb**; component IV: positions **Eb, est** and **esb**). Besides, the impacts coincide in the position **V** (for components II and III) and **Eb** (for components III and IV). It means that there are some cases of polymorphism where the variation in **Est** and **Esb** is connected with **V** (component II), and variation in **est** and **esb** is connected with **Eb** (component IV). Such case appears, for the component II, in South African genus *Hadogenes* (Ischnuridae) (high polytrichy: 27 trichobothria in **V** and up to 30 in **Est + Esb**; we shall see below that the same trend in **V** position is common in "type" C).
For the component IV, the trend is a reduction of positions **est, esb** and **Eb** in some buthid genera (*Karasbergia, Lissothus, Microbuthus, Pectini-*

buthus). All these genera are taxonomically distant from each other, thus trends of reduction are independent.

Although the mechanisms of reduction or increasing of the sensory apparatus elements are unknown, we must note that all the mentioned genera are inhabiting arid areas and have very specific adaptations: *Microbuthus* is found in the intertidal zone (Vachon 1950), *Lissothus* and *Pectinibutus* inhabit sand deserts (Vachon 1952; Fet 1987), *Karasbergia* burrows underground and *Hadogenes* inhabits rock crevices (Lamoral 1979).

Thus, the ancestral trend of reduction of trichobothria in certain positions that was in charge of splitting of three basic "types" A, B and C, evidently was employed sometimes later, but only within the "type" A (Buthidae).

Principal component III: This component describes only polytrichy within "type C", both in manus and tibia. (Tab. 3, Fig. 2). Variations in manus involve three positions: **i, Eb** and **V**. Only one case of polythrichy in **i** is recorded: 5 trichobothria instead of 2 in a South American genus *Teuthraustes* (Chactidae). The cases of polytrichy in **Eb** position of manus are known for *Brachistosternus* (Bothriuridae), and in **V** position for several genera to the different degrees: *Centromachetes* (Scorpionidae), *Vachonia* and *Timogenes* (Bothriuridae), *Heteroscorpion* (Ischnuridae), *Euscorpius* (Chactidae), *Scorpiops* (Vaejovidae).

In all these cases, polytrichy in **V** position does not involve other positions in manus, but in *Vachonia, Euscorpius* and *Scorpiops* it is accompanied by polytrichy in the position **v** in tibia. Here, a connection in embryonic development of ventral neurons leading to trichobothria both in tibia and manus is not improbable. In the component III, the positive impact of variations in **v** and **e** (excluding **eb**)(tibia) and in **V** (manus), is "compensated" by negative impact of variations in **eb** (tibia) and **Eb** (manus) (Tab. 3).

"Compensation" in **Eb** is found only in *Brachystosternus* (polytrichy from 2 to 5 trichobothria). "Compensation" in **e** (tibia) is local this character in general gives positive impact, but the formation of two subseries (**eb** and **eba**) can be observed on the basis of one common series. In "types" A and B, position **eba** is not distinguished at all (**eb** = 2); in "orthobothriotaxic" genera of "type" C, **eb** = 5; when accessory trichobothria appear (in *Broteas, Broteochactas, Euscorpius, Megacormus, Plesiochactas*), **eb + eba** can increase to 12 (sometimes also **eb** decrease to 3 or 4).

The most common and general trend of polymorphism described by the principal component III is the gradual polytrichy in tibia and manus in "type" C (in "type" A, some genera may have polytrichy in tibia [*Liobuthus* and *Vachoniolus*] and in femur [*Buthiscus*], but PCA does not reveal any significant relationships here). Polytrichy in **V, v** and **e**, hardly detectable in Ischnuridae (Madagascan *Heteroscorpion*) and in some South American Chactidae, approaches its highest degree in South Asian *Scorpiops* (Vaejovidae, Scorpiopsinae) and Mediterranean *Euscorpius* (Chactidae, Euscorpiinae). These two last genera are supposed to be taxonomically close to each other and also to American subfamily Megacorminae (Chactidae)(Fet 1985; Sissom 1990). These three subfamilies probably should be pooled to form a separate family; here we regard to this complex, provisorily as to "euscorpiids". A lot of taxonomical controversy

exists about these subfamilies and about the families Chactidae and Vaejovidae in general (Sissom 1990). The case of "euscorpiids" deserves a more detailed description because it probably represents the most recent events in the evolution of trichobothrial patterns.

"Euscorpiid" complex includes following genera: *Euscorpius, Dasyscorpiops, Megacormus, Parascorpiops, Plesiochactas, Scorpiops* and *Troglocormus*. These lineages should have been diverged at least since the early Tertiary (concluding from the existence of an endemic genus *Parascorpiops* from Borneo and some endemic American genera). From these genera, only *Euscorpius* and *Scorpiops* have variations in the position V of manus; other genera are limited to the variations in tibia (as in some other genera from Chactidae and Vaejovidae). These variations (polytrichy) in manus may represent the more recent mechanism of polymorphism that existed in some "latent" form in a common ancestor of both Mediterranean (*Euscorpius*) and South East Asian (*Scorpiops*) branches and later was "activated" independently. Such "activation" also can be connected with ventral neuron of tibia, as in the mentioned genus *Vachonia* (Bothriuridae). In "euscorpiids", in the position V of manus, only polytrichous variations exist: from 4 to 6 trichobothria in *Euscorpius* (*Tetratrichobothrius*) from 8 to 11 in *Euscorpius* (*Polytrichobothrius*) and from 10 to 11 in *Scorpiops* (*Alloscorpiops*).

In all "euscorpiids", similar trends in variations in tibia are found. the ancestral number should be about $v = 6$ and $e = 17$, i.e. about 26 trichobothria in all surfaces of tibia. The "saltatoric" polytrichy is represented here by Malaysian genus *Dasyscorpiops*, with $v = 14$ and $e = 59$! (this genus was not included to our statistical analysis, because territories within e series were not distinguished in literature). In *Euscorpius* and *Scorpiops*, the number of trichobothria in position v and e also varies within subgenera and even within species; this variation is a subject of a separate study. The most polymorphic genera in the whole order, *Euscorpius* and *Scorpiops*, are found in the areas of recent glaciation, at mountain regions of Europe and Asia. Some of the species are found in (unusual for scorpions) cold highland habitats at Alps and Himalayas. Their considerable cold-hardiness and the ability to form isolated populations are the features of advanced recent evolutionary changes, e.g. in *Euscorpius germanus marcuzzii* (Bonacina 1980), a variety that has refugial origin of glacial times.

Within the "type C", the most deviant from basic "orthobothriotaxy" patterns are found: first, in two "saltatoric polytrichous" genera (*Vachonia* and *Hadogenes*); second, in an entire "euscorpiid" complex. All other genera of the "type C" do not show great deviation from "ortho"-pattern, which is true for virtually the entire families Bothriuridae, Ischnuridae, Scorpionidae, Diplocentridae, Iuridae, Chactidae (excluding Euscorpiinae and Megacorminae) and Vaejovidae (excluding Scorpiopsinae).

The mechanisms of polytrichy probably are ancient (as exhibited by the trichobothria of manus in the basic splitting into "types A, B and C") but still active up to the most recent times, for example in the glacial-time polymorphism in *Euscorpius,* where polytrichy involved only tibial positions v and e, but not the position V in manus. It looks like a mechanism existing in a latent form and "turning on" its different parts to provide polytrichy.

Generally, two major trends of trichobothrial polymorphism are observed in scorpions. The first is polytrichy (which may be either gradual or immediate, "saltatoric"). The second is reduction of a single trichobothria (or, rarely, "duplication"). The trend of polytrichy evidently corresponds to the polymerization of sensory organs (here, of a trichobothrial set). Reduction or duplication are quite different from the polytrichy. The case of duplication seems to be a local event (in femor or in the pedipalp finger), without any evidence of further polymerization. The reduction of trichobothria can be an oligomerization event leading to the integration of a sensory system.

The principal component analysis demostrates that these two trends of variation are independent within two general branches of scorpions: buthoids (reduction and duplication) and scorpionoids (polytrichy). Undoubtedly, oligotrichy in scorpionoids is ancestral. M. Vachon (1974) was definitely right considering oligotrichous genera of scorpionoids to be "orthobothriotaxic". In the most evolutionary advanced families of so-called katoikogeneous scorpions (Scorpionidae, Ischnuridae and Diplocentridae) (Sissom 1990), oligotrichous condition is symplesiomorphic.

Modifications of trichobothriotaxy are more often observed in manus rather than in tibia or femur of pedipalp. There can be certain behavioral and/or ecological reasons for this: obviously, the manus is closer to the substrate and experiences the major mechanical pressure; in scorpions it is used not only as sensory organ but for the most active grasping, digging etc. In different genera and species, according to their behavior, different surfaces and "territories" of manus may be exposed to the environmental factors. This provides the highest variability of trichobothria in this segment of pedipalp.

CONCLUSIONS:

1. The variation of trichobothrial patterns in scorpions is described by four principal components which determine about 80% of the variance.
2. Four principal components (I, II, III and IV) describe the following independent trends of variation:
(I) the ancestral divergence into three "types" of trichobothriotaxy (A, B and C) described by Vachon (1974);
(II) saltatoric polytrichy in "type C";
(III) gradual polytrichy in "type C";
(IV) reduction in "type A".
3. The most important trend of polymorphism in modern scorpions is gradual polytrichy. Within the "euscorpiid" complex (Euscorpiinae + Scorpiopsinae + Megacorminae), gradual polytrichy is especially significant, which may be an additional confirmation of phylogenetic proximity of these three subfamilies.

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