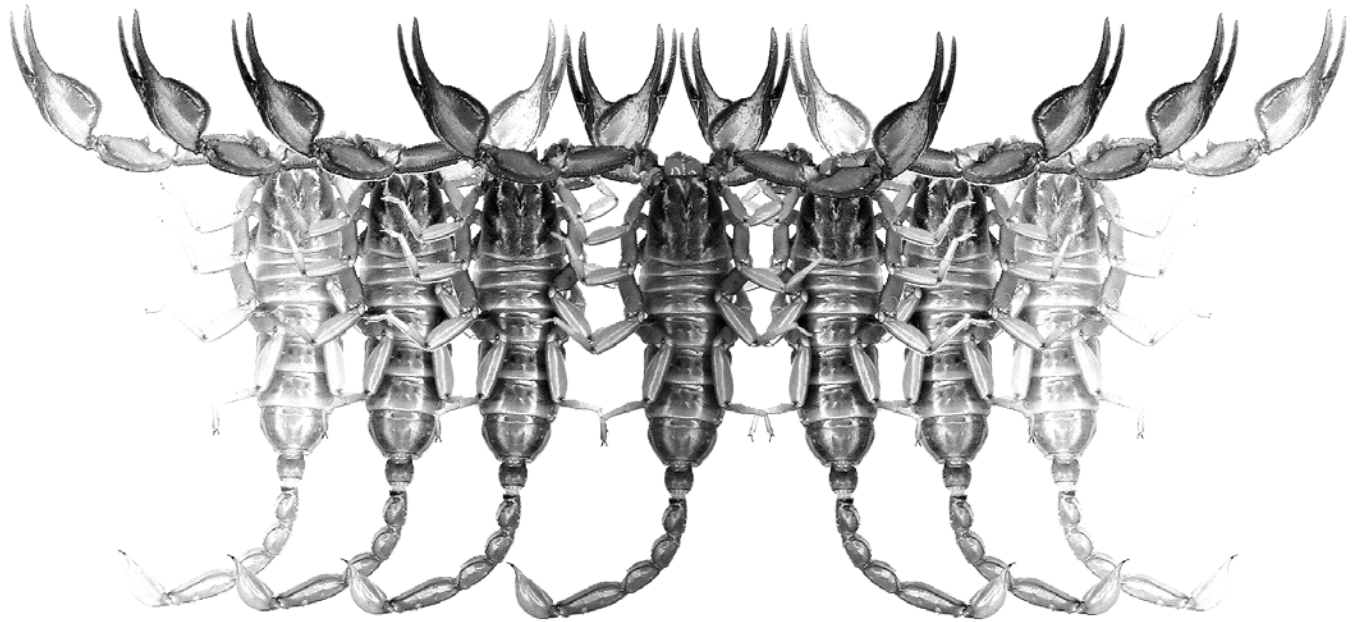


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A New Trichobothrial Character for the High-Level Systematics of Buthoidea (Scorpiones: Buthida)

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A new trichobothrial character for the high-level systematics of Buthoidea (Scorpiones: Buthida)

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Summary

The high-level systematics and phylogeny of the scorpion superfamily Buthoidea are unresolved. A new, formerly undetected character is reported here: the relative alignment of d_3 trichobothrium and DM_c carina on the pedipalp patella. This and other characters are discussed in the context of possible high-level divisions of Buthoidea. Based on this analysis, we suggest a breakdown of Buthoidea into six proposed tentative phylogenetic groups: *Buthus* group, *Ananteris* group, *Isometrus* group, *Charmus* group, *Uroplectes* group, and *Tityus* group.

Introduction

The high-level systematics and phylogeny of the scorpion superfamily Buthoidea are unresolved (Soleglad & Fet, 2003b; Coddington et al., 2004). The superfamily currently includes 88 valid genera of extant and fossil scorpions, among them a number of genera containing the most toxic known scorpion species. The monophyly of Buthoidea (the only superfamily of parvorder Buthida) is well demonstrated; among many other character sets, it is supported by so-called trichobothrial type A (Vachon, 1974; Soleglad & Fet, 2001, 2003b). However, the relationship between two buthoid families, Buthidae and Microcharmidae, remains unclear (Fet, 2000; Soleglad & Fet, 2003b).

Fet & Lowe (2000) discussed the historical attempts to recognize subfamilies in Buthidae using a limited set of various diagnostic characters (Kraepelin, 1899, 1905; Birula, 1917a, 1917b, etc.). Currently, subfamilies in Buthidae are not recognized (Stahnke, 1972; Sissom, 1990; Fet & Lowe, 2000) since there is no consensus about the diagnostic criteria.

Vachon (1975) introduced a new character for high-level systematics of Buthidae, which separates all Buthoidea into two groups, *alpha* and *beta*, according to the mutual position of trichobothria d_1 – d_3 – d_4 on the dorsal aspect of pedipalp femur, and in part, the surface location of trichobothrium d_2 . This grouping did not correspond to any of the subfamily subdivisions proposed by the earlier authors.

Here, we report a new, formerly undetected character: the relative position of d_3 trichobothrium and dorsomedian carina (DM_c) on the pedipalp patella. The importance of the DM_c carina as a synapomorphy of Buthoidea was demonstrated by Soleglad & Fet (2003b) and was used recently as the primary character for the placement of fossil scorpion *Uintascorpio* in family Buthidae (Santiago-Blay et al., 2004b). However, the position of patellar trichobothria has not been sufficiently studied so far. In relation to the DM_c carina, trichobothrium d_3 can be located internally (i.e. between the dorsointernal (DI_c) and DM_c carinae) or externally (i.e. between the DM_c and dorsoexternal (DE_c) carinae). The distribution of the new character appears to split all genera of Buthoidea in two major groups. Below, we provide the first comparative study of this character as it relates to the *alpha/beta* pattern in Buthoidea and discuss its phylogenetic implications.

Based on the cladistic analysis presented in this paper, we propose six tentative phylogenetic groupings within the superfamily Buthoidea: ***Buthus*** group, ***Ananteris*** group, ***Isometrus*** group, ***Charmus*** group, ***Uroplectes*** group, and the ***Tityus*** group. (The bold font is used here and elsewhere in this paper solely for better visual comprehension, not because we assign to it any official taxonomic value). Individual genus placements within these six groups are stated in Table 1 where they are correlated with the characters discussed in this paper. As will be shown, these six hypothesized phylogenetic groups of buthoids and their interrelationships are delineated, in part, by the small set of fundamental charac-

ters discussed in this paper. Although predictively, these groups are not completely defined by the small character set presented herein, we believe they do in fact represent a reasonable partitioning of Recent buthoid scorpions and will, in our opinion, further enhance future discussions involving the systematics of this highly complicated group. The small set of characters and information on biogeographical associations of these six buthoid groups are provided below.

Methods & Material

Terminology and conventions

Terminology describing pedipalp chelal ornamentation follows that described and illustrated in Soleglad & Sissom (2001). Terminology for the pedipalp patella follows that described in Soleglad & Fet (2003b). Terminology for the orthobothriotaxic types follows that described in Vachon (1974) and Soleglad & Fet (2001), and terminology for the sternum is that of Soleglad & Fet (2003a).

Note, as stated above, we follow the designations of buthoid trichobothria as established by Vachon (1974); however, we follow homology of these trichobothria across orthobothriotaxic types as established by Soleglad & Fet (2001). It is important to note that in Soleglad & Fet (2001: 9–10), different designations were employed in some cases in order to emphasize suggested trichobothrium homology between fossil and Recent scorpions, but, as these authors stated, the purpose was not to consolidate and/or change the accepted designations as originally established by Vachon (1974).

Cladistic analysis software packages

Software package PAUP* Version 4 (beta) (Swofford, 1998) was used for Maximum Parsimony (MP) analysis of morphology-based character codings. Cladograms from PAUP* were generated by TreeView (Win 32) Version 1.5.2 (Page, 1998).

Abbreviations

List of depositories: AMNH, American Museum of Natural History, New York, New York, USA; CAS, California Academy of Sciences, San Francisco, California, USA; GL, Personal collection of Graeme Lowe, Philadelphia, Pennsylvania, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MES, Personal collection of Michael E. Soleglad, Borrego Springs, California, USA; MHNG, Muséum d'histoire naturelle de la Ville de Genève, Geneva, Switzerland; NMB, Naturhistorisches Museum

Basel, Basel, Switzerland; USNM, United States National Museum, Smithsonian Institution, Washington, DC, USA; VF, Personal collection of Victor Fet, Huntington, West Virginia, USA; WDS, Personal collection of W. David Sissom, Texas, USA; ZMH, Zoologisches Museum Hamburg, Hamburg, Germany.

Material examined

The following buthoid material was examined for analysis and/or illustrations provided in this paper. Refer to this section for locality and gender data of species-level illustrations.

Buthidae: *Alayotityus nanus* Armas, 1973, Santiago, Cuba, (VF); *Androctonus bicolor* Ehrenberg, 1828, Lhav, Israel, ♂ (MES); *Androctonus crassicauda* (Olivier, 1807), Duhai, Oman, ♂ (GL); *Anomalobuthus rickmersi* Kraepelin, 1900, Bukhara, Uzbekistan, ♂♀ (VF); *Apistobuthus pterygocercus* Finnegan, 1932, Oman, (VF); *Buthacus yotvatensis* Levy, Amitai & Shulov, 1973, Abu Dhabi, United Arab Emirates, ♂ (VF); *Butheolus anthracinus* (Pocock, 1897), Dhofar, Oman, ♂ (GL); *Butheolus gallagheri* Vachon, 1980, Oman, ♂ (GL); *Butheolus thalassinus*, Ta'izz, Yemen, ♂ (WDS); *Buthus occitanus* Amoreux, 1789, Casablanca, Morocco, (MES); *Centruroides bicolor* (Pocock, 1898), Quepos, Costa Rica, ♂ (GL); *Centruroides elegans* (Thorell, 1876), Ixtapan, Guerrero, Mexico, ♀ (MES); *Centruroides exilicauda* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♀ (MES); *Centruroides hentzi* (Banks, 1910), Panama City, Florida, USA, ♀ (MES); *Centruroides infamatus ornatus* Pocock, 1902, Tamazula, Jalisco, Mexico, ♀ (MES); *Centruroides koesteri* Kraepelin, 1911, Puntarenas, Costa Rica, ♀ (GL); *Centruroides limbatus* (Pocock, 1898), Limon, Costa Rica, ♀ (GL); *Centruroides limpidus* (Karsch, 1879), Oaxtepec, Morelos, Mexico, ♀ (GL); *Centruroides margaritatus* (Gervais, 1841), Panama, ♂ (MES); *Centruroides nigrescens* (Pocock, 1898), Oaxaca, Mexico, ♂♀ (GL); *Centruroides nigrovariatus baergi* Hoffmann, 1932, Tehuacan, Puebla, Mexico, ♀ (MES); *Centruroides noxius* Hoffmann, 1932, Tepic, Nayarit, Mexico, ♀ (MES); *Centruroides pallidiceps* Pocock, 1902, Mazatlan, Sinaloa, Mexico, ♀ (MES); *Centruroides sculpturatus* Ewing, 1928, Caborca, Sonora, Mexico, ♀ (MES); *Centruroides vittatus* (Say, 1821), Cuatro Ciénegas, Coahuila, Mexico, ♂ (MES); *Compsobuthus acutecarinatus* (Simon, 1882), Oman, ♀ (GL); *Compsobuthus brevimanus* (Werner, 1936), Sana'a, Yemen, ♂ (WDS); *Compsobuthus maindroni* (Kraepelin, 1900), Hajar al Sharqi, Oman, ♀ (GL); *Compsobuthus matthiesseni* (Birula, 1905), Baghdad, Iraq, (VF); *Compsobuthus polisi* Lowe, 2001, Wadi Dirif, Oman, holotype ♂ (NMB); *Compsobuthus rugosulus* (Pocock, 1900), Tatta,

	d_3/DM_c		DM_c/d_3		
	Beta		Beta		Alpha
	$d_2(d)$	$d_2(d)$	$d_2(i)$	$d_2(d)$	$d_2(i)$
Buthus group (39 genera)					
<i>Androctonus</i> , <i>Anomalobuthus</i> , <i>Apistobuthus</i> , <i>Baloorthochirus</i> , <i>Birulatus</i> , <i>Buthacus</i> , <i>Butheolus</i> , <i>Buthiscus</i> , <i>Buthus</i> , <i>Cicileus</i> , <i>Compsobuthus</i> , <i>Congobuthus</i> , <i>Darchenia</i> , <i>Hemibuthus</i> , <i>Hottentotta</i> , <i>Iranobuthus</i> , <i>Kraepelinia</i> , <i>Lanzatus</i> [*] , <i>Leiurus</i> , <i>Liobuthus</i> [*] , <i>Lissothus</i> ¹ , <i>Mesobuthus</i> , <i>Microbuthus</i> ¹ , <i>Neobuthus</i> , <i>Odontobuthus</i> , <i>Orthochiroides</i> , <i>Orthochirus</i> ² , <i>Paraorthochirus</i> , <i>Pectinibuthus</i> [*] , <i>Plesiobuthus</i> [*] , <i>Polisius</i> , <i>Psammobuthus</i> , <i>Razianus</i> , <i>Sabinebuthus</i> [*] , <i>Sassanidothus</i> , <i>Simonoides</i> , <i>Somalibuthus</i> , <i>Vachoniolus</i> [*] , <i>Vachonus</i>	X				
Ananteris group (6 genera)					
<i>Akentrobuthus</i> [*] , <i>Ananteris</i> , <i>Himalayotityobuthus</i> , <i>Lychas</i> , <i>Lychasioides</i> , <i>Microananteris</i>		X			
Isometrus group (7 genera)					
<i>Afroisometrus</i> [*] , <i>Australobuthus</i> , <i>Babycurus</i> , <i>Hemilychas</i> , <i>Isometroides</i> , <i>Isometrus</i> [*] , <i>Odonturus</i>			X		
Charmus group (3 genera)					
<i>Charmus</i> , <i>Somalicharmus</i> , <i>Thaicharmus</i>				X	
Uroplectes group (18 genera)					
<i>Ankaranocharmus</i> ¹ , <i>Butheoloides</i> , <i>Buthoscorpio</i> , <i>Egyptobuthus</i> , <i>Grosphus</i> , <i>Karasbergia</i> ¹ , <i>Microcharmus</i> , <i>Neogrosphus</i> , <i>Neoprotobuthus</i> , <i>Palaeogrosphus</i> , <i>Parabuthus</i> , <i>Pseudolissothus</i> , <i>Pseudolychas</i> , <i>Pseudouroplectes</i> , <i>Tityobuthus</i> , <i>Troglotityobuthus</i> , <i>Uroplectes</i> , <i>Uroplectoides</i>					X
Tityus group* (9 genera)					
<i>Alayotityus</i> ¹ , <i>Centruroides</i> [*] , <i>Mesotityus</i> [*] , <i>Microtityus</i> ^{2*} , <i>Rhopalurus</i> [*] , <i>Tityopsis</i> [*] , <i>Tityus</i> [*] , <i>Troglorhopalurus</i> [*] , <i>Zabius</i> ^{1*}					X

Table 1: Fundamental trichobothrial pattern characters for superfamily Buthoidea (82 Recent genera) partitioned into six groups: patellar d_3 position with respect to dorsomedian (DM_c) carina (i.e., *internal* or *external* to carina); and femoral *alpha/beta* pattern with special emphasis on the position of trichobothrium d_2 (i.e., *dorsal* surface or *internal* surface). (d) = dorsal surface of femur; (i) = internal surface of femur. * Tibial spurs absent; ¹ Femur trichobothrium d_2 absent, or, ² d_2 vestigial to absent.

Pakistan, ♀ (CAS); *Compsobuthus weneri* (Birula, 1908), Dintorni di Ju Amlah, Yemen, ♀ (WDS); *Grosphus hirtus* Kraepelin, 1901, Tamatave Province, Perinet, Madagascar, ♀ (MES); *Grosphus madagascariensis* (Gervais, 1843), Anjiro, Madagascar, ♂ (GL); *Hottentotta hottentotta* (Fabricius, 1787), North Province, Cameroon, ♀ (GL); *Hottentotta jayakari* (Pocock, 1895), between Seeb & Al Khod, Oman, ♂ (GL); *Hottentotta judaicus* (Simon, 1872), Jerusalem, Israel, ♀ (MCZ); *Hottentotta minax* (L. Koch, 1875), Eritrea, ♂ (VF); *Hottentotta trilineatus* (Peters, 1861), S. Magadi, Kenya, ♂ (GL); *Isometroides vesicus* (Karsch, 1880), South Australia, Australia, ♀ (GL); *Isometrus maculatus* (DeGeer, 1778), Diego Garcia, Indian Ocean, (MES), Honolulu Co., Hawaii, USA, ♀ (GL); *Isometrus melanodactylus* (L. Koch, 1867), New South Wales, Australia, ♂ (GL); *Isometrus* sp., Papua New Guinea, ♀ (MES); *Kraepelinia palpator* (Birula, 1903), Badghyz, Turkmenistan, ♀ (VF); *Leiurus quinquestriatus* (Ehrenberg,

1828), Saudi Arabia, (VF); *Liobuthus kessleri* Birula, 1898, Chardara, Kazakhstan, ♀ (VF); *Lychas marmoreus*, South Australia, Australia, ♂ (GL); *Lychas* sp., Viti Levu, Fiji, ♀ (MES); *Lychas* sp., Indonesia, (VF); *Mesobuthus caucasicus* (Nordmann, 1840), Chardara, Kazakhstan, ♀ (VF); *Microbuthus* sp., Rusail, Oman, ♂ (GL); *Odontobuthus doriae* (Thorell, 1877), Kachan, Iran, ♀ (CAS); *Odontobuthus odonturus* (Pocock, 1897), Indus delta, Pakistan, ♀ (AMNH); *Orthochirus scrobiculosus* (Grube, 1873), Israel, (MES); *Parabuthus granulatus* (Ehrenberg, 1831), Rehoboth, RSA, ♂ (GL); *Parabuthus liosoma* (Ehrenberg, 1828), Sodora, Ethiopia, ♂ ♀ (GL); *Parabuthus pallidus* Pocock, 1895, Lodwar Kenya, ♀ (GL); *Parabuthus transvaalicus* Purcell, 1899, Beitbridge, Zimbabwe, ♂ (GL); *Parabuthus* sp., Kenya, ♀ (VF); *Paraorthochirus glabrifrons* (Kraepelin, 1903), Muscat, Oman, holotype (ZMH); *Polisius persicus* Fet, Capes & Sissom, 2001, Zahedan, Iran, ♂ (USNM); *Razianus zarudnyi* (Birula, 1903), Gachsaran,

Fars, Iran, (VF); *Rhopalurus junceus* (Herbst, 1800), Camaquey, Sibanidi, Cuba, ♀ (VF); *Tityus championi* Pocock, 1898, Puntarenas, Costa Rica, ♂ (GL); *Tityus dedoslargos* Francke et Stockwell, 1987, Quepos, Costa Rica, ♂♀ (GL); *Tityus ecuadorensis* Kraepelin, 1896, Vilcabamba, Ecuador, ♂ (GL); *Tityus nematochirus* Mello-Leitão, 1940, Bucaramango, Colombia, ♂ (MES); *Tityus ocelote* Francke et Stockwell, 1987, Quepos, Costa Rica, ♂ (GL); *Uroplectes planimanus* (Karsch, 1879), Maun, Botswana, ♂ (GL); *Uroplectes vittatus* (Thorell, 1876), Doddiebun, Zimbabwe, ♂ (VF), Nata, Botswana, ♀ (GL).

Microcharmidae: *Microcharmus hauseri* Lourenço, 1996, Lokobe Natural Reserve, Île Nosy Be, Madagascar, holotype ♂ (MHNG).

Character Analysis

Soleglad & Fet (2003b), in their high-level analysis of Recent scorpion systematics, established the dorsomedian (DM_c) carina of the pedipalp patella as a synapomorphy for parvorder Buthida. In the same analysis, they expanded the definition of the important femoral trichobothria arrangement, *alpha/beta*, as originally established by Vachon (1975). In this paper, we expand further on these two character structures and, for the first time, present an important new character, the arrangement of the patellar dorsal trichobothria d_1 – d_5 , in particular, trichobothrium d_3 , as they relate to the DM_c carina.

DM_c carina. Vachon (1952: Figs. 66–68) illustrated eight carinae for the pedipalp patella in his section on scorpion morphology nomenclature. Based on the analysis of Soleglad & Fet (2000b: 52–58), it turned out that these eight carinae (the largest number of carinae occurring on the patella in any known Recent scorpion) applied to the buthoids *only*, in particular, the dorsomedian (DM_c) carina which is unique to the buthoids. In Vachon's (1952) analysis, the overwhelming majority of taxa described were buthoids (the only other scorpions discussed were *Euscorpium* (superfamily Chactoidea) and *Scorpio* (superfamily Scorpionoidea)), therefore this unique carina, termed “*médiane dorsale*”, was included in Vachon's nomenclature.

Santiago-Blay et al. (2004b: Fig. 5–7) used the DM_c carina as the primary character for placing the Eocene fossil scorpion *Uintascorpio halandrasorum* Perry, 1995 in the family Buthidae. In this paper Santiago-Blay et al. (2004b: 8) further verified the existence of the DM_c carina for 32 extant buthoid genera based on specimen examination, roughly 40 % of all currently described genera. In this paper, based on existing literature, 20 additional buthoid genera were verified as having the DM_c carina, bringing the total to 52 genera, 63 % of described Recent buthoid genera. It must be noted here,

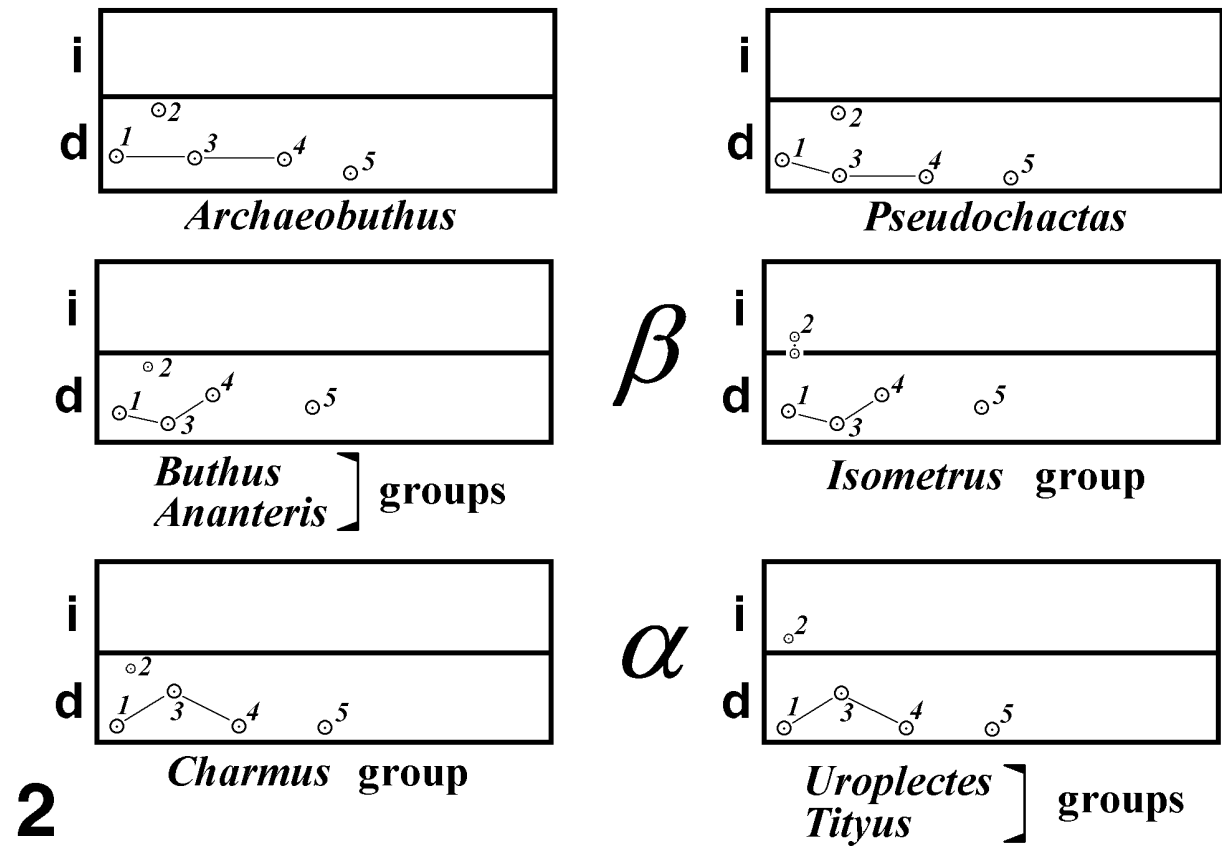
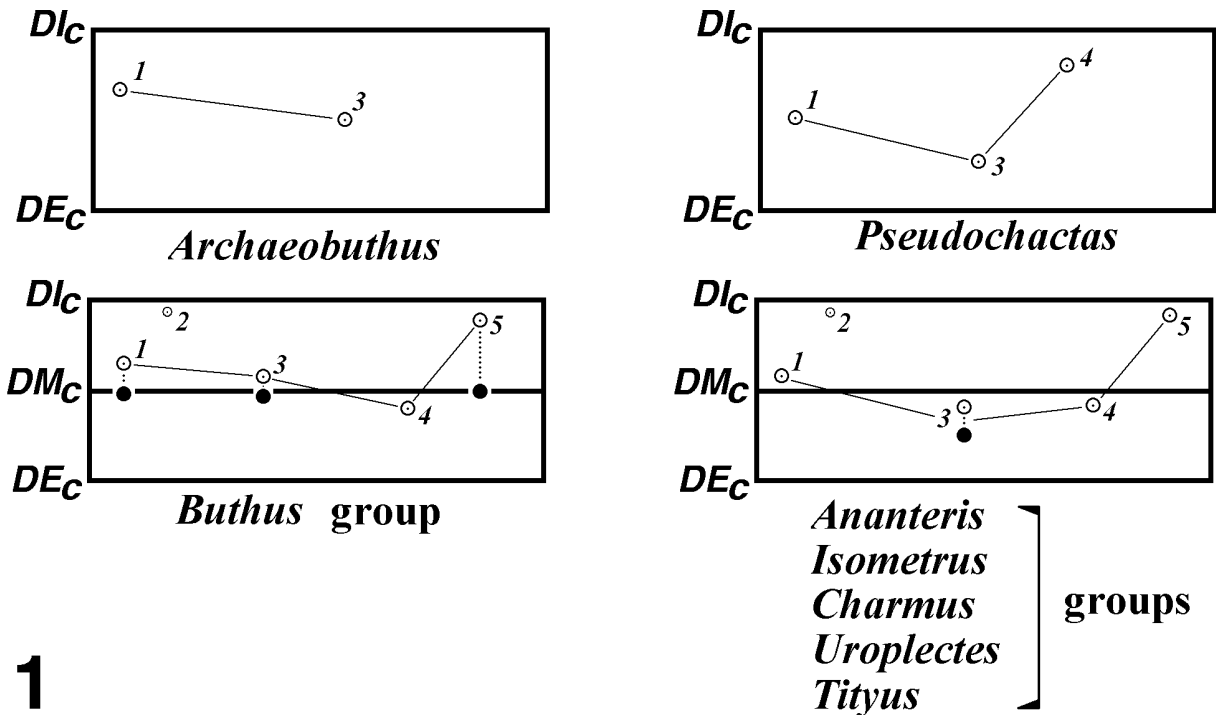
however, that not all authors necessarily illustrated the DM_c carina, especially if it is somewhat smooth in its structure, or in cases where carinae were not illustrated at all. Therefore, we suspect that in the remaining genera which could not be verified, many will prove to have this unique carina.

Soleglad & Fet (2003b) established that outgroup taxon *Pseudochactas ovchinnikovi* (Pseudochactidae) does not have the DM_c carina (Fig. 3). They hypothesized that the Carboniferous family Palaeopisthacanthidae also lacked this carina, based on a partial description of the patella of fossil scorpion *Composcorpius elegans* by Jeram (1994b); i.e., they exhibited the *seven carinae configuration*, hypothesized as primitive for Recent scorpions. In the same analysis, Soleglad & Fet (2003b) stipulated that the outgroup species *Archaeobuthus estephani* exhibited this unique carina, based entirely on the figure provided by Lourenço (2001b: Fig. 13). However, after a recent reanalysis of the type specimen (Santiago-Blay et al., in preparation) we have concluded that the existence of the DM_c carina in *Archaeobuthus* cannot be determined one way or the other. We discuss this further in the section on cladistic analysis.

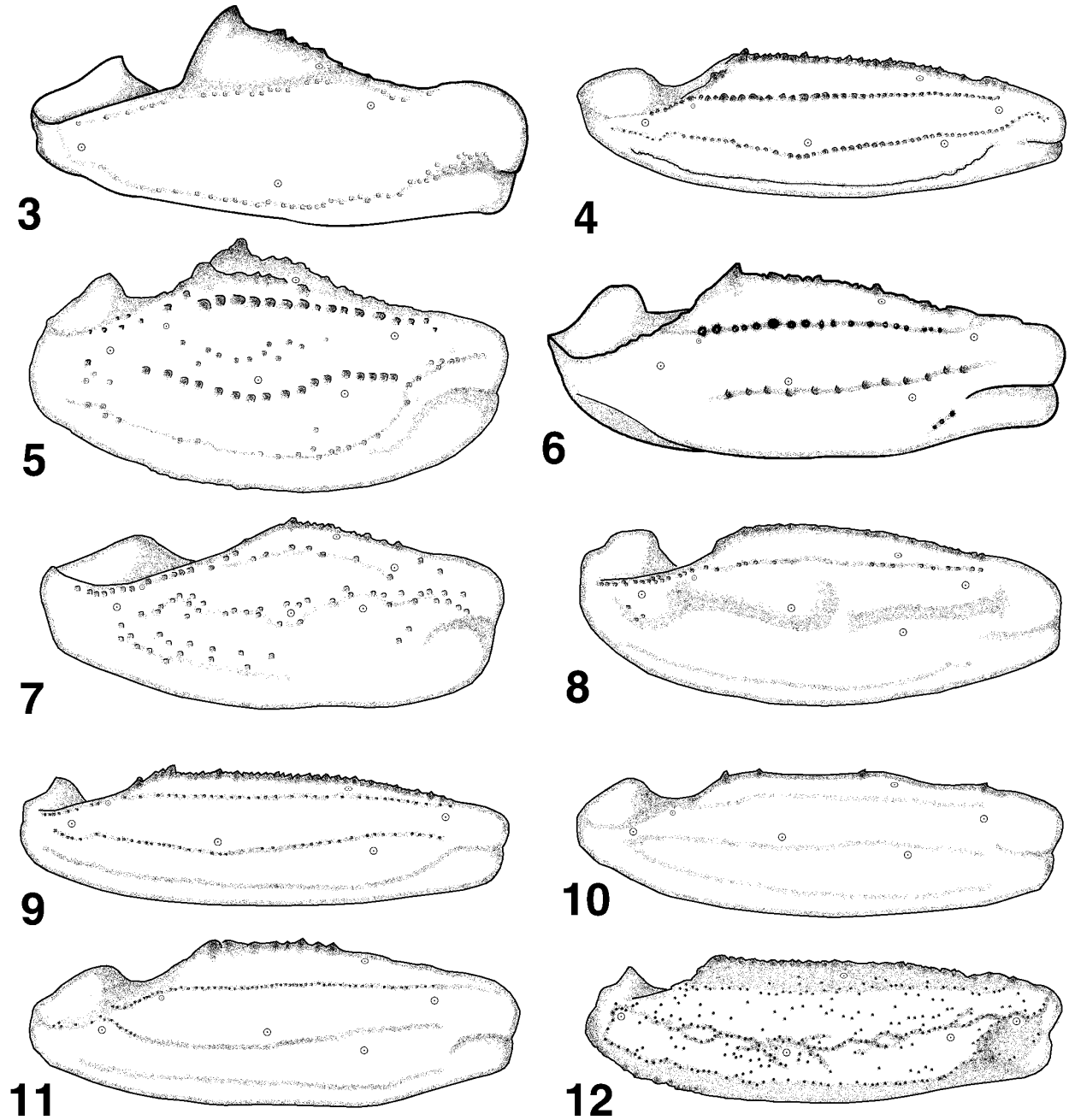
DM_c and trichobothrium d_3 alignment. Vachon (1974: Figs. 30–36) defined the orthobothriotaxic Type A trichobothrial pattern for the buthoids. This pattern is a major synapomorphy for the parvorder Buthida (Soleglad & Fet, 2003b), as are the other fundamental patterns established by Vachon (1974) for other high-level Recent scorpion groups (i.e., Type B, parvorder Chaerilida; Type C, parvorder Lurida; and Type D, parvorder Pseudochactida, the latter orthobothriotaxic type defined by Soleglad & Fet, 2001: Fig. 13). In the Type A pattern, we find five dorsal trichobothria located on the patella, d_1 – d_5 , with trichobothrium d_2 being petite in size.

In a detailed analysis of the patella of Recent buthoid genera, including available specimens and the ample volume of existing literature, we were able to confirm two basic alignments of the dorsal patellar trichobothria as they relate to the DM_c carina: trichobothrium d_3 is positioned on the dorsal surface either “internally” (i.e., between the dorsointernal (DI_c) and DM_c carinae), or it is located “externally” (i.e., between the DM_c and dorsoexternal (DE_c) carinae). That is, the DM_c carina horizontally bisects the dorsal surface of the patella. In general, this orientation is *consistent* within a genus and, as important, the collection of genera compliant to these two d_3 – DM_c arrangements are congruent to the *alpha/beta* pattern as defined by Vachon (1975). That is, this character is important phylogenetically, which we discuss in detail in the **Cladistic analysis** section below.

Figure 1 shows four configurations of the patellar dorsal trichobothrial patterns as they relate to the dorsal carinae. The two outgroup taxa, *Archaeobuthus* and *Pseudochactas*, exhibit a subset of the Type A dorsal



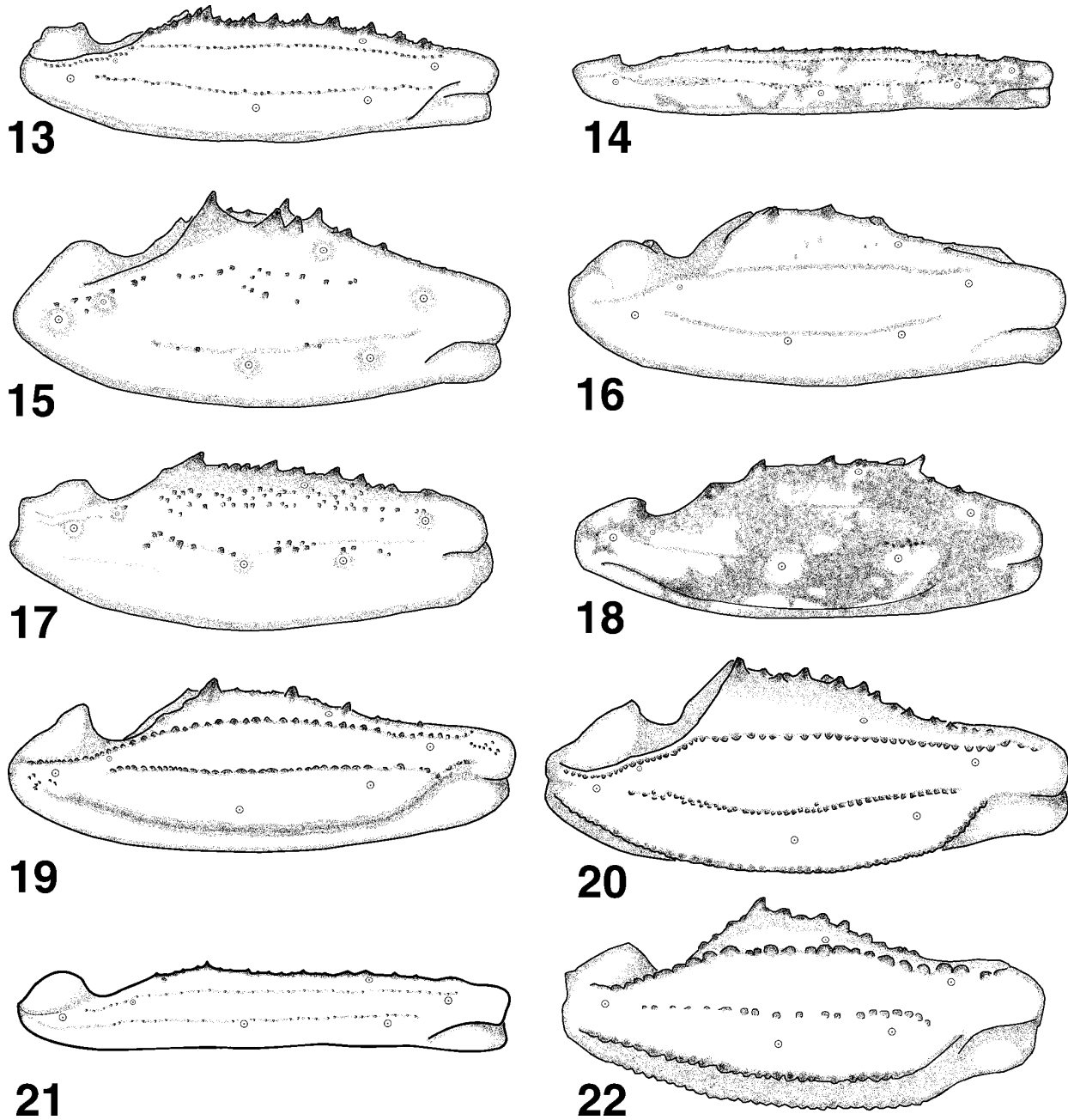
Figures 1-2: Schematic diagram of pedipalp patella (dorsal surface) and femur (dorsal and internal surfaces) illustrating important trichobothrial arrangements. **1.** Patella. Note, closed circles depict alternative positions for indicated trichobothria as follows: *Microbuthus* in *Buthus* group (lower left) and *Tityus* group (lower right). DI_c = dorsointernal carina, DM_c = dorsomedian carina, DE_c = dorsoexternal carina **2.** Femur. i = internal, d = dorsal; α = alpha, β = beta.



Figures 3-12: Pedipalp patella, dorsal view, showing the alignment of trichobothrium d_3 with respect to the dorsomedian (DM_c) carina. In the buthoid figures d_3 is situated *internal* to or *on* the DM_c carina. **3.** *Pseudochactas ovchinnikovi* (after Soleglad & Fet, 2003b, in part) Note, DM_c carina is absent as well as trichobothria d_2 and d_4 . **4.** *Androctonus bicolor*. **5.** *Razianus zarudnyi*. **6.** *Mesobuthus caucasicus* (after Soleglad & Fet, 2003b, in part). **7.** *Liobuthus kessleri*. **8.** *Orthochirus scrobiculosus*. **9.** *Compsobuthus matthiesseni*. **10.** *Anomalobuthus rickmersi*. **11.** *Buthacus yotvatensis*. **12.** *Microbuthus* sp. Note, trichobothrium d_3 bifurcates the DM_c carina and trichobothrium d_2 is absent. Only trichobothria i and d_1 - d_5 are shown in these figures.

trichobothria, their hypothesized homology with the buthoid Type A pattern being based on Soleglad & Fet (2001: Fig. 3). Also, in the two outgroups, the DM_c carina is depicted as absent (Figs. 1 and 3). For the buthoids, two configurations are distributed across the six proposed groups of genera as follows:

Exclusively in the *Buthus* group, the trichobothrium d_3 is located internally on the dorsal surface (rarely positioned on the DM_c carina, see *Liobuthus* and *Microbuthus* below); this accounts for no less than 39 genera. In this pattern only trichobothrium d_4 is consistently located externally on the surface. Figs. 4-12 illustrate this



Figures 13-22: Pedipalp patella, dorsal view, showing the alignment of trichobothrium d_3 with respect to the dorsomedian (DM_c) carina. In these figures, d_3 is situated *external* to the DM_c carina. **13.** *Lychas* sp. **14.** *Isometrus maculatus*. **15.** *Grosphus hirtus*. **16.** *Parabuthus* sp. **17.** *Uroplectes vittatus*. **18.** *Microcharmus hauseri*, holotype. **19.** *Centruroides margaritatus* (after Santiago-Blay et al., 2004b, in part). **20.** *Rhopalurus junceus* (after Santiago-Blay et al., 2004b, in part). **21.** *Tityus nematochirus* (after Soleglad & Fet, 2003b, in part). **22.** *Alayotityus nanus* (note trichobothrium d_2 is absent). Only trichobothria i and d_1-d_5 are shown in these figures.

pattern for nine major genera in the *Buthus* group. These figures show various degrees of development of the DM_c carina, from a well delineated crenulate carina in genera *Androctonus* (Fig. 4), *Razianus* (Fig. 5), *Mesobuthus* (Fig. 6) and *Compsobuthus* (Fig. 9); to irregularly defined as in *Orthochirus* (Fig. 8), *Liobuthus*

(Fig. 7) and *Microbuthus* (Fig. 12); and to weak or smooth as in genera *Anomalobuthus* (Fig. 10) and *Buthacus* (Fig. 11). The alignment of the dorsal trichobothria in genus *Microbuthus* (Figs. 1, 12; Vachon, 1952: Figs. 470, 471; Lourenço, 2002: Fig. 16) is very interesting: we see d_1 , d_3 , d_4 and d_5 are found either on or

external to the DM_c carina. In particular, d_3 (Fig. 12, Lourenço, 2002: Fig. 16) is sometimes located in a “dimple” bifurcating, in part, the DM_c carina. In many buthoids exhibiting an internally placed d_3 , we see that the DM_c carina angles externally somewhat at the position of d_3 's location (e.g., Figs. 4, 5, 7, 8, and 9). In particular, d_3 in *Liobuthus* (Fig. 7) is located in a dimple bifurcating the DM_c carina, similar to that seen in *Microbuthus*. The placement of trichobothrium d_5 in *Microbuthus* is unprecedented in the buthoids. This placement appears to be caused, in part, by the internal tapering of the DM_c carina at the distal aspect of the patella, a little more exaggerated than that seen in other genera; but we also note that d_3 is not positioned as close to the dorsointernal (DI_c) carina as in other genera exhibiting either d_3 - DM_c alignment. Finally, the unique configuration exhibited in *Microbuthus* may also be the product of the DM_c carina slightly repositioning in an internal direction on the patellar surface. This hypothesis is further supported by the inline to external position of trichobothria d_1 , d_3 and d_5 with respect to the DM_c carina.

In the other five groups of genera, *Ananteris*, *Isometrus*, *Charmus*, *Uroplectes* and *Tityus* (comprising 43 genera), the trichobothrium d_3 is positioned externally on the dorsal surface. Figures 13–22 illustrate this pattern for four of the five groups complying to this pattern (members of the *Charmus* group were not available). In these figures are included the genus *Microcharmus* (Fig. 18), presently assigned to family Microcharmidae; *Lychas* (Fig. 13), a member of the *Ananteris* group; *Isometrus* (Fig. 14), member of the *Isometrus* group; plus genera from the *Uroplectes* and *Tityus* groups. In this pattern, two trichobothria, d_3 and d_4 , are situated external to this carina. As in the *Buthus* group, one can observe different degrees of development in the DM_c carina: well developed and granulate as in genera *Lychas* (Fig. 13), *Isometrus* (Fig. 14), *Uroplectes* (Fig. 17), and the four members of the *Tityus* group; and smooth and/or irregular as in genera *Grosphus* (Fig. 15), *Parabuthus* (Fig. 16), and *Microcharmus* (Fig. 18). In the *Tityus* group, the trichobothrium d_3 is located more external from the DM_c carina than the other groups (Fig. 1). In three of the four genera illustrated for the *Tityus* group, we see that trichobothrium d_3 is located considerably external to the DM_c carina. Note that for the species *Tityus nematochirus* (Fig. 21), d_3 is situated quite close to this carina, but we attribute this to the extreme slenderness of the species. In other *Tityus* species illustrated in the literature, d_3 is positioned as illustrated here for genera *Centruroides* (Fig. 19), *Rhopalurus* (Fig. 20), and *Alayotityus* (Fig. 22).

We also see other tendencies in trichobothria positions on the patella as it relates to the two alignments of d_3 : in the *Buthus* group trichobothrium d_1 is located slightly internal to the DM_c carina whereas in the other

alignment, d_1 is located roughly inline with DM_c . In the *Buthus* group, the d_1 - d_3 - d_4 juncture is either formed in a straight line, or angles upward towards the DI_c carina, whereas in the other alignment, the d_1 - d_3 - d_4 juncture angles downward towards the DE_c carina. In both configurations, trichobothrium d_4 is located external to DM_c .

The assignment of the genera to the two d_3 - DM_c alignments is based on the analysis of actual specimens as well as illustrations in available literature. For actual specimens, the representatives of five out of six groups were available (members of the *Charmus* group were not available for examination), in total 28 genera and 71 species. Including literature sources, we have confirmed these alignments in 68 genera (out of 82 total Recent genera defined in Buthoidea) spanning 407 species. For those cases where either the DM_c carina is vestigial, or, not illustrated in a particular figure, we made determination based on the relative position of d_3 on the dorsal surface of the patella. In general, for members of the *Buthus* group, trichobothrium d_3 is located roughly mid-segment from a vertical perspective, and, in members of the other groups, d_3 is located lower on the segment. With respect to actual specimens we encountered no exceptions to the groupings defined above. Any presumed exceptions where found in literature illustrations only (these are discussed in the **Database** section). Also, in many genera, the DM_c carina was illustrated for some species and not for others. In these cases, the position of d_3 on the patella was generally consistent.

We consider this character to be significant since it involves a trichobothrium “migrating” across a carina. Although one can detect some minor dislocations of individual trichobothria on the pedipalp surface, in general the overall topology of trichobothria distribution is quite constant thus providing excellent characters for the diagnoses of many taxonomic levels in scorpions. However, those minor dislocations never involve a trichobothrium moving across a carina, and therefore, we consider the latter to be a significant evolutionary event. There are several other important examples of this phenomenon in Recent scorpions: (1) the movement of chelal trichobothrium Et_2 to the ventral surface in the bothriurids (superfamily Scorpionoidea), traversing the ventroexternal (VI) carina; (2) chelal trichobothrium V_4 dislocation to the external surface in many euscorpids (superfamily Chactoidea), migrating across the VI carina; (3) chelal trichobothrium Eb_1 moving to the ventral surface in many chactids (superfamily Chactoidea), again, crossing VI ; (4) patellar trichobothrium v_3 moving to the external surface in the vaejovids (superfamily Chactoidea) and the iuroids (superfamily Iuroidea), traversing the VE_c carina; and (5) patellar trichobothrium v_2 moving to the external surface in the typhlochactines (superfamily Chactoidea) across the VE_c carina. All of these examples are considered synapomorphies for these groups (Soleglad & Fet, 2003b).

Alpha/beta pattern. Vachon (1975) established the femoral *alpha/beta* trichobothrial pattern for the Type A configuration, specifically relevant to the buthoids. This somewhat simple observation on trichobothrial positions appears to be quite important in the high-level systematics of the Buthoidea. For example, Sissom (1990: 93) used this pattern as his primary couplet in his extensive key to buthoid genera (albeit, the key was not necessarily intended to be phylogenetic). Soleglad & Fet (2001) discussed this basic pattern as it related to the fossil scorpion *Archaeobuthus* and Recent scorpion *Pseudochactas*. These two species did not comply specifically with either *alpha* or *beta* patterns as originally defined by Vachon, although all five dorsal trichobothria present in these taxa were considered homologous to those found in Buthoidea (Soleglad & Fet, 2001). In their effort to determine the phylogenetic position of the primitive scorpion *Pseudochactas*, Soleglad & Fet (2003b) divided the original *alpha/beta* pattern into three subpatterns which would accommodate the patterns of both *Pseudochactas* and the fossil scorpion *Archaeobuthus*; the genus *Chaerilus* (superfamily Chaeriloidea) was also considered. We adopt this refinement of the *alpha/beta* pattern as well in this paper [note: alignment with respect to the dorsoexternal carina is from a *midsegment* perspective]:

- *Alpha/beta* subpattern: alignment of d_1-d_3
 - parallel to dorsoexternal carina (primitive)
 - points toward dorsoexternal carina (β)
 - points away from dorsoexternal carina (α)
- *Alpha/beta* subpattern: alignment of d_3-d_4
 - parallel to dorsoexternal carina (primitive)
 - points away from dorsoexternal carina (β)
 - points toward dorsoexternal carina (α)
- *Alpha/beta* subpattern: placement of d_2
 - on dorsal surface (primitive and β)
 - on internal surface (α)

In Vachon's (1975: Figs. α , β) original definition for the *alpha* pattern, trichobothria d_1-d_3 point away from, and d_3-d_4 point toward the dorsoexternal carina, and d_2 is located on the internal surface. In contrast, these conditions are reversed in the *beta* pattern. In *Archaeobuthus*, $d_1-d_3-d_4$ trichobothria are essentially in a straight line, thus both subpattern alignments are parallel to the dorsoexternal carina, and d_2 is located on the dorsal surface, all of which Soleglad & Fet (2003b) hypothesized as primitive states. *Pseudochactas* exhibits the same pattern as *Archaeobuthus* except d_1-d_3 points toward the dorsoexternal carina, which is a *beta* pattern characteristic. It was demonstrated by Soleglad & Fet (2003b: Fig. 115), using *Archaeobuthus* and *Pseudo-*

chactas as outgroups to the Buthoidea, that the *beta* pattern, in part, is primitive and the *alpha* pattern is a derivation from the *beta* pattern. In addition, also based on *Archaeobuthus* and *Pseudochactas*, Soleglad & Fet (2003b) considered the dorsal positioning of d_2 to be primitive in the buthoids, and therefore, the internal position of d_2 is derived.

In Figure 2 we illustrate the femoral trichobothrial pattern for *Archaeobuthus*, *Pseudochactas* and two versions each of the buthoid *alpha/beta* pattern. In Fig. 2 the *beta* pattern is divided into two subpatterns, the "pure" *beta*, where d_2 is positioned dorsally, which is found in the *Buthus* and *Ananteris* groups (i.e., this pattern conforms to the original definition of Vachon, 1975); and the "diluted" *beta*, where d_2 is positioned either on the dorsointernal carina or the internal surface of the femur, which is found in the *Isometrus* group. We have an analogous situation with the *alpha* pattern: the "pure" *alpha*, where d_2 is positioned on the internal surface, found in the *Uroplectes* and *Tityus* groups (i.e., this pattern conforms to the original definition of Vachon, 1975); and the "diluted" *alpha*, where d_2 exists on the dorsal surface, found in the *Charmus* group.

The determination of trichobothrial positions in the buthoids is a difficult task since, in general, individual trichobothria are somewhat smaller in size in this superfamily than in other Recent scorpions. Determining the position of trichobothrium d_2 is even a more difficult task since it is petite in size. This is further complicated by the somewhat narrow tapering basal aspect of the pedipalp femur. In our examination of the literature illustrations we found only two genera where more than one species was depicted with trichobothrium d_2 located on the dorsointernal carina, *Isometrus* and *Parabuthus*. In most of these cases, this was purely a judgment call since this carina is somewhat underdeveloped on the extreme basal portion of the segment. However, the stated difficulties aside, we do believe the distinctions described herein and illustrated in Fig. 2 are legitimate and provide additional information on the evolution of these five femoral trichobothria.

Other observations of patellar trichobothria. During the analysis of the d_3-DM_c alignment, we also conducted a preliminary analysis of the configuration of the seven external patellar trichobothria with respect to the exteromedian (EM_c) carina. Based on literature only (in most part, specimens were not examined for this preliminary analysis) we concluded that trichobothria *est*, *esb₁*, and *eb₁* are located on the dorsal half of the segment whereas trichobothria *et*, *em*, *esb₂*, and *eb₂* are found on the ventral half of the segment, both sets of trichobothria being separated by the EM_c carina (consistent with Vachon's, 1974: Fig. 35, original depiction of the Type A pattern). We found no examples where a trichobothrium had migrated across this carina from either set, as is the case with trichobothrium d_3 and DM_c .

However, we did detect an interesting configurational difference: in the *Tityus* group, and, in part, the *Uroplectes* group, the trichobothrial series esb_1 – esb_2 are substantially separated from each other, the angle formed by esb_1 – esb_2 angling considerably towards the distal aspect of the segment (i.e., esb_2 is positioned closer to trichobothrium *em* than is esb_1); in contrast, in other groups of genera, esb_1 – esb_2 are in close proximity, essentially parallel from a horizontal perspective (assuming the patella is positioned vertically). Genera complying to these two configurations of the esb_1 – esb_2 series (based mostly on literature and some specimen examinations) are as follows:

esb_1 – esb_2 in close proximity, essentially parallel.

***Buthus* group:** *Anomalobuthus*, *Buthacus*, *Buthoscorpio*, *Buthus*, *Compsobuthus*, *Hottentotta*, *Krapelinia*, *Leiurus*, *Liobuthus*, *Mesobuthus*, *Microbuthus*, *Neobuthus*, *Paraorthochirus*, *Polisius*, *Razianus* and *Vachoniolus*. ***Ananteris* group:** *Ananteris* and *Lychas*; ***Isometrus* group:** *Isometrus* (esb_1 – esb_2 exhibits some slight angling distally); ***Charmus* group:** *Charmus*, *Thaicharmus* (exhibits medium angling distally).

esb_1 – esb_2 not in close proximity, esb_2 positioned more distally.

***Uroplectes* group:** *Butheoloides*, *Grosphus*, *Parabuthus* (in part), *Tityobuthus*, *Uroplectes*, and *Uroplectoides*; ***Tityus* group:** *Alayotityus* (slight angling) *Centruroides*, *Mesotityus*, *Microtityus*, *Rhopalurus*, *Tityus*, and *Zabius* (as in *Alayotityus*, this genus esb_2 is only slightly positioned above esb_1 ; Luis Acosta, personal observation based on literature).

It must be stressed here that these observations are based on preliminary data only. In addition, it is important to note that minor localized dislocation of patellar trichobothria, especially in a vertical direction, is somewhat common in scorpions (whereas migration of a trichobothrium across a carina is not). Therefore, this data must be solidified with more genera and species in order to ascertain if these two esb configurations are important in any major phylogenetic sense. It does seem clear, however, based on this preliminary analysis alone, that it probably is valid for the New World *Tityus* group, where the pattern is the most exaggerated, and possibly for the Old World *Uroplectes* group as well. If this holds true, then we have another synapomorphy for the clade (*Uroplectes* group + *Tityus* group), both of these groups exclusively exhibiting a “pure” form of the *alpha* pattern.

Tibial spurs. The tibial spur is considered an important character in scorpion systematics. In particular it has been considered a major character in buthoid taxonomy. Sissom (1990: 93–100) used the presence/absence

of this spur as a second-level couplet in no less than three places in his key to buthoid genera. Although the tibial spur is present in many fossil scorpions—e.g., *Compsoscorpium* (Jeram, 1994a: Text-Fig. 5-D), *Palaeoburmesebuthus* (Santiago-Blay et al. 2004a), *Pulmonoscorpium* (Jeram, 1994b)—there is a great variability in Recent scorpions. In the primitive parvorders, the tibial spurs are present on legs III–IV in Pseudochactida (presumably plesiomorphic), absent in Chaerilida, and variable in Buthida. In Buthida, tibial spurs are absent in New World genera, and variable within the Old World members, although showing consistency across many genera. We consider the consistent *loss* of the tibial spur in the New World buthids, all exclusively members of the *Tityus* group, an important derivation. We do not, however, consider the scattered loss of the tibial spurs in the Old World buthids necessarily important phylogenetically. Table 1 shows that tibial spur loss occurs in three Old World groups, the ***Buthus***, ***Ananteris***, and ***Isometrus*** groups. Furthermore, in certain Old World psammophilic genera (e.g., *Anomalobuthus*, *Apistobuthus*, *Liobuthus*, *Pectinibuthus*, *Plesiobuthus*, *Sabinebuthus*, *Vachoniolus*, etc.) we see either a reduction or the complete absence of these spurs, presumably a factor of microhabitat adaptation (Fet et al., 1998). The independent DNA-based phylogeny of Fet et al. (2003) for 17 genera of Buthidae demonstrated the polyphyletic origin of psammophily among these genera; the full or partial tibial spur loss is observed independently in at least three lineages including psammophilic genera *Anomalobuthus*, *Liobuthus*, and (*Vachoniolus* + *Apistobuthus*). In addition, as reported by Soleglad & Fet (2003b), the tibial spur appears to be a vestigial structure in Recent scorpions, since it exhibits little or no structure within the membrane from which it extends (personal observation of Graeme Lowe on *Apistobuthus*). This observation, of course, is based only on a single species, but one might assume, if it holds true for the superfamily in general, that due to its vestigial nature it is highly susceptible to loss or near loss due to microhabitat pressures. Finally, we might add that the tibial spur exhibited in fossil scorpions probably was not vestigial, perhaps performing some adaptive function.

Database

The list below includes 82 currently valid genera of Buthoidea (Soleglad et al., 2005, with additions from Lourenço, 2000g, 2003a, 2004a) partitioned in the hypothesized groups. For each genus, we partition the data into groups where the DM_c carina is visible and where it is not. For the genera marked with an asterisk (*), the position of d_3 with respect to DM_c has still to be verified since no drawings of dorsal patella were available in literature. The number of species evaluated per genus is stated. In addition, we characterize six known fossil

genera of Buthidae. For those few examples where apparent exceptions to the two patellar trichobothria alignments occur, they are noted as such. These exceptions are discussed individually at the end of this section.

Note: for the genera whose d_3 - DM_c alignment is not known, we tentatively stipulate their group association based on close affinity to other genera, geographic locality, and/or other characters. Clearly, the alignment for these genera must be determined before final group placement can be established.

Since in a large majority of cases presented below the data are consistent within a genus, we consider these data as an empirical “proof” of the legitimacy of the new character described in this paper.

Patellar trichobothrium d_3 internal to carina DM_c

“*Buthus* group”. Trichobothrial pattern *beta*, femur trichobothrium d_2 located dorsally (39 genera); tibial spur is lost in *Lanzatus*, *Liobuthus*, *Pectinibuthus*, *Plesiobuthus*, *Sabinebuthus*, and *Vachoniolus*.

Androctonus Ehrenberg, 1828 (12 species): DM_c visible: *A. amoreuxi* (Audouin, 1826) (Vachon, 1952: Fig. 218; Vachon, 1958: Fig. 2); *A. amoreuxi levyi* Fet, 1997 (Levy & Amitai, 1980: Fig. 45, as *A. a. hebraeus*); *A. australis* (Linnaeus, 1758) (Vachon, 1952: Fig. 203; Levy & Amitai, 1980: Fig. 41); *A. baluchicus* Pocock, 1900 (Lourenço, 2005b: Fig. 15); *A. bicolor* Ehrenberg, 1828 (Fig. 4, specimen examined; Vachon, 1952: Figs. 159, 166, as *A. aeneas*; Levy & Amitai, 1980: Fig. 37, as *A. b. bicolor*; Lourenço, 2005b: Fig. 34); *A. crassicauda* (Olivier, 1807) (Vachon, 1952: Fig. 172; Levy & Amitai, 1980: Fig. 33; specimen examined); *A. dekeyseri* Lourenço, 2005 (Lourenço, 2005b: Fig. 29); *A. gonneti* Vachon, 1948 (Lourenço, 2005b: Fig. 9); *A. hoggarensis* (Pallary, 1929) (Vachon, 1952: Fig. 194; Lourenço, 2005b: Fig. 45); *A. liouvillei* (Pallary, 1924) (Lourenço, 2005b: Fig. 37); *A. maelfaiti* Lourenço, 2005 (Lourenço, 2005b: Fig. 21); *A. mauritanicus* (Pocock, 1902) (Vachon, 1952: Fig. 177; Lourenço, 2005b: Fig. 41); *A. sergenti* Vachon, 1948 (Vachon, 1952: Fig. 191; Lourenço, 2005b: Fig. 47).

Anomalobuthus Kraepelin, 1900 (one species): DM_c visible: *A. rickmersi* Kraepelin, 1900 (Fig. 10, specimen examined).

Apistobuthus Finnegan, 1932 (one species): DM_c visible: *A. pterygocerus* Finnegan, 1932 (Vachon, 1960a: Fig. 2; Lourenço, 1998b: Fig. 4; specimen examined).

**Baloorthochirus* Kovařík, 1996 (= *Pakistanorthochirus* Lourenço, 1997) (placed here since the genus is close to *Orthochirus*; see Kovařík, 1996, 2004).

Birulatus Vachon, 1974 (one species): DM_c visible: *B. astartiae* Stathi et Lourenço, 2003 (Stathi & Lourenço, 2003: Fig. 8).

Buthacus Birula, 1908 (ten species): DM_c visible: *B. clevai* Lourenço, 2001 (Lourenço, 2001c: Fig. 21); *B. mahraouii* Lourenço, 2004 (Lourenço, 2004g: Fig. 8); *B. villiersi* Vachon, 1949 (Vachon, 1952: Fig. 248); *B. yotvatensis* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 33; Fig. 11; Levy & Amitai, 1980: Fig. 84; Fig. 11, DM_c visible as smooth carina in specimen examined). DM_c not visible: *B. arenicola* (Simon, 1885) (Vachon, 1952: Fig. 256; Levy & Amitai, 1980: Fig. 80); *B. foleyi* Vachon, 1948 (Vachon, 1952: Fig. 236); *B. huberi* Lourenço, 2001 (Lourenço, 2001c: Fig. 8); *B. leptochelys* (Ehrenberg, 1829) (Vachon, 1952: Fig. 263; Levy & Amitai, 1980: Fig. 73; Lourenço, 2004c: Fig. 13); *B. leptochelys nitzani* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 22; Levy & Amitai, 1980: Fig. 77); *B. yotvatensis nigroaculeatus* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 39); *B. striffleri* Lourenço, 2004 (Lourenço, 2004c: Fig. 4); *B. zieglerei* Lourenço, 2000 (Lourenço, 2000c: Fig. 6), **exception**, d_3 external to DM_c .

Butheolus Simon, 1882 (three species): DM_c visible: *B. gallagheri* Vachon, 1980 (specimen examined); *B. thalassinus* Simon, 1882 (Sissom, 1994: Fig. 11; specimen examined). DM_c not visible: *B. anthracinus* (Pocock, 1897) (specimen examined).

Buthiscus Birula, 1905 (one species): DM_c visible: *B. bicalcaratus* Birula, 1905 (Vachon, 1952: Fig. 113; Lourenço, 2002b: Fig. 5).

Buthus Leach, 1815 (eight species): DM_c visible: *B. atlantis* Pocock, 1889 (Vachon, 1952: Fig. 356); *B. bonito* Lourenço et Geniez, 2005 (Lourenço & Geniez, 2005: Fig. 6); *B. draa* Lourenço et Slimani, 2004 (Lourenço & Slimani, 2004: Figs. 3, 6); *B. ibericus* Lourenço et Vachon, 2004 (Lourenço & Vachon, 2004: Fig. 36); *B. jianxinae* Lourenço, 2005 (Lourenço, 2005a: Fig. 3); *B. maroccanus* Birula, 1903 (Vachon, 1952: Fig. 369); *B. montanus* Lourenço et Vachon, 2004 (Lourenço & Vachon, 2004: Fig. 26); *B. occitanus* (Amoreux, 1789) (Vachon, 1952: Figs. 342, 389, 390, 404, 413, 424, 429, 441, 446; Lourenço & Vachon, 2004: Fig. 8; specimen examined); *B. occitanus israelis* (Shulov et Amitai, 1959) (Levy & Amitai, 1980: Fig. 28).

Cicileus Vachon, 1948 (two species): DM_c visible: *C. cloudsleythompsoni* Lourenço, 1999 (Lourenço, 1999d: Fig. 6); *C. exilis* (Pallary, 1928) (Vachon, 1952: Fig. 96).

Compsobuthus Vachon, 1949 (17 species): DM_c visible: *C. acutecarinatus* (Simon, 1882) (Vachon, 1940a:

- Fig. 9, as *Buthus*; Sissom, 1994: Fig. 16; specimen examined); *C. andresi* Lourenço, 2004 (Lourenço, 2004d: Fig. 5); *C. arabicus* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 18); *C. brevimanus* (Werner, 1936) (Sissom, 1994: Fig. 22; specimen examined); *C. carmelitus* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 2; Levy & Amitai, 1980: Fig. 66); *C. garyi* Lourenço et Vachon, 2001 (Lourenço & Vachon, 2001: Fig. 8); *C. jordanensis* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 12); *C. longipalpis* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 8; Levy & Amitai, 1980: Fig. 69); *C. maindroni* (Kraepelin, 1900) (specimen examined); *C. matthiesseni* (Birula, 1905) (Sissom & Fet, 1998: Fig. 5; Fig. 9, specimen examined); *C. polisi* Lowe, 2001 (Lowe, 2001: Fig. 7); *C. rugosulus* (Pocock, 1900) (Lourenço & Monod, 1998: Fig. 5; specimen examined); *C. simoni* Lourenço, 1999 (Lourenço, 1999e: Fig. 14); *C. tofti* Lourenço, 2001 (Lourenço, 2001d: Fig. 6); *C. vachoni* Sissom, 1994 (Sissom, 1994: Fig. 35); *C. werneri* (Birula, 1908) (Vachon, 1952: Fig. 289; Levy & Amitai, 1980: Fig. 60; Sissom, 1994: Fig. 29 specimen examined); *C. werneri schmiedeknechti* Vachon, 1949 (Levy & Amitai, 1980: Fig. 60, as *C. w. judaicus*); *C. williamsi* Lourenço, 1999 (Lourenço, 1999e: Fig. 8).
- Congobuthus** Lourenço, 1999 (one species): **DM_c visible:** *C. fagei* Lourenço, 1999 (Lourenço, 1999c: Fig. 12)
- *Darchenia** Vachon, 1977 (placed here since the genus is close to *Compsobuthus*; see Lourenço, 1995).
- Hemibuthus** Pocock, 1900 (one species): **DM_c visible:** *H. crassimanus* Pocock, 1900 (Vachon, 1960b: Fig. 2; Tikader & Bastawade, 1983: Fig. 297).
- Hottentotta** Birula, 1908 (12 species): **DM_c visible:** *H. acostai* Lourenço, 2004 (Lourenço, 2004b: Fig. 6); *H. alticola kabulensis* Vachon, 1958 (Vachon, 1958: Fig. 14, as *Buthotus*); *H. arenaceus* (Purcell, 1901) (Lamoral, 1979: Fig. 48, as *Buthotus*); *H. conspersus* (Thorell, 1877) (Lamoral, 1979: Fig. 69, as *Buthotus*); *H. franzwerneri* (Birula, 1914) (Vachon, 1952: Fig. 326, as *Buthotus*); *H. hottentotta* (Fabricius, 1787) (Vachon, 1940a: Fig. 3, as *Buthus*; specimen examined); *H. minax* (L. Koch, 1875) (specimen examined); *H. judaicus* (Simon, 1872) (Vachon, 1952: Fig. 319, as *Buthotus*; Levy & Amitai, 1980: Fig. 55, as *Buthotus*; specimen examined); *H. socotrensis* (Pocock, 1889) (Vachon, 1979: Fig. 3, as *Buthotus*); *H. trilineatus* (Peters, 1861) (specimen examined). **DM_c not visible:** *H. geffardi* Lourenço, 2000 (Lourenço, 2000b: Fig. 2); *H. jayakari* (Pocock, 1895) (specimen examined).
- Iranobuthus** Kovařík, 1997 (one species): **DM_c visible:** *I. krali* Kovařík, 1997 (Kovařík, 1997b: Fig. 10).
- Kraepelinia** Vachon, 1974 (one species): **DM_c visible:** *K. palpator* (Birula, 1903) (Vachon, 1974: 236; specimen examined)
- Lanzatus** Kovařík, 2001 (one species): **DM_c not visible:** *L. somalicus* Kovařík, 2001 (Kovařík, 2001: Fig. 5).
- Leiurus** Ehrenberg, 1828 (two species): **DM_c visible:** *L. jordanensis* Lourenço, Modry et Amr, 2002 (Lourenço et al., 2002: Fig. 5); *L. quinquestriatus* (Ehrenberg, 1828) (Vachon, 1952: Fig. 275; Sissom, 1994: Fig. 41; specimen examined); *L. quinquestriatus hebraeus* (Birula, 1908) (Levy & Amitai, 1980: Fig. 50).
- Liobuthus** Birula, 1898 (one species): **DM_c visible:** *L. kessleri* Birula, 1898 (Fig. 7, specimen examined).
- Lissothus** Vachon, 1948 (one species): **DM_c not visible:** *L. bernardi* Vachon, 1944 (Vachon, 1952: Fig. 126); **femur trichobothrium d₂ absent** (placed here tentatively due to general morphology and biogeographic connections).
- Mesobuthus** Vachon, 1950 (eight species): **DM_c visible:** *M. caucasicus* (Nordmann, 1840) (Fig. 6, specimen examined); *M. caucasicus parthorum* (Pocock, 1900) (Vachon, 1958: Fig. 33); *M. eupeus haarlovi* Vachon, 1958 (Vachon, 1958: Fig. 43); *M. marten-sii* (Karsch, 1879) (Qi et al., 2004: Fig. 12); *M. songi* Lourenço, Qi et Zhu, 2005 (Lourenço et al., 2005b: Fig. 13); *M. tamulus gangeticus* (Pocock, 1900) (Tikader & Bastawade, 1983: Fig. 597); *M. tamulus gujaratensis* (Pocock, 1900) (Tikader & Bastawade, 1983: Fig. 572). **DM_c not visible:** *M. hendersoni* (Pocock, 1900) (Tikader & Bastawade, 1983: Fig. 647); *M. pachyurus* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 698); *M. rugiscutis* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 672); *M. tamulus* (Fabricius, 1798) (Vachon, 1940b: Fig. 15, as *Buthus grammurus*; Tikader & Bastawade, 1983: Fig. 621); *M. tamulus concanensis* (Pocock, 1900) (Tikader & Bastawade, 1983: Fig. 523); *M. tamulus indicus* (Pocock, 1900) (Tikader & Bastawade, 1983: Fig. 547).
- Microbuthus** Kraepelin, 1898; **femur trichobothrium d₂ absent** (three species): **DM_c visible:** *M. fagei fagei* Vachon, 1949 (Vachon, 1952: Fig. 470); *M. fagei marocannus* Lourenço, 2002 (Lourenço, 2002a: Fig. 16); *M. pusillus* Kraepelin, 1898 (Vachon, 1952: Fig. 471; Lourenço, 2002a: Fig. 12); *M. sp.* (Fig. 12, specimen examined).
- Neobuthus** Hirst, 1911 (two species): **DM_c not visible:** *N. cloudsleythompsoni* Lourenço, 2001 (Lourenço, 2001h: Fig. 17); *N. sudanensis* Lourenço, 2005 (Lourenço, 2005a: Fig. 24).
- Odontobuthus** Vachon, 1950 (three species): **DM_c visible:** *O. bidentatus* Lourenço et Pézier, 2002 (Lourenço & Pézier, 2002a: Fig. 26); *O. doriae* (Thorell, 1877) (specimen examined). **DM_c not visible:** *O. odonturus* (Pocock, 1897) (specimen examined).

- Orthochiroides** Kovařík, 1998 (one species): **DM_c visible:** *O. vachoni* Kovařík, 1998 (Kovařík, 1998: Fig. 17).
- Orthochirus** Karsch, 1891 (seven species): **DM_c visible:** *O. afghanus* Kovařík, 2004 (Kovařík, 2004: Fig. 3; **DM_c** not shown?); *O. bicolor* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 346); *O. flavescens* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 314); *O. innesi* Simon, 1910 (Vachon, 1952: Fig. 306); *O. krischnai* (Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 362); *O. pallidus* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 330); *O. scrobiculosus negebensis* (Shulov et Amitai, 1960) (Fig. 8, specimen examined; Levy & Amitai, 1980: Fig. 89).
- Paraorthochirus** Lourenço & Vachon, 1997 (four species): **DM_c visible:** *P. glabrifrons* (Kraepelin, 1903) (type specimen examined); *P. goyffoni* Lourenço et Vachon, 1995 (Lourenço & Vachon, 1995: Fig. 15); *P. kinzelbachi* Lourenço et Huber, 2000 (Lourenço & Huber, 2000: Fig. 7); *P. stockwelli* Lourenço et Vachon, 1995 (Lourenço & Vachon, 1995: Fig. 9).
- Pectinibuthus** Fet, 1984 (one species): **DM_c not visible:** *P. birulai* Fet, 1984 (Fet, 1987: Fig. 4).
- Plesiobuthus** Pocock, 1900 (one species): **DM_c visible:** *P. paradoxus* Pocock, 1900 (Capes & Fet, 2001: Fig. 3).
- Polisius** Fet, Capes et Sissom, 2001 (one species): **DM_c visible:** *P. persicus* Fet, Capes et Sissom, 2001 (Fet et al., 2001: Fig. 4).
- ***Psammobuthus** Birula, 1911 (this genus is a possible synonym of *Anomalobuthus*; A. Gromov, pers. comm., 2002).
- Razianus** Farzanpay, 1987 (= *Neohemibuthus* Lourenço, 1996) (one species): **DM_c visible:** *R. zarudnyi* (Birula, 1903) (Fig. 5, specimen examined; Lourenço, 1996d: Fig. 6, as *Neohemibuthus kinzelbachi*).
- ***Sabinebuthus** Lourenço, 2001 (placed here since the genus is close to *Anomalobuthus*; see Lourenço, 2001a).
- ***Sassanidothrus** Farzanpay, 1987 (placed here since the genus is close to *Mesobuthus*; see Vachon, 1958)
- ***Simonoides** Vachon et Farzanpay, 1987 (placed here since the genus is close to *Orthochirus*).
- ***Somalibuthus** Kovařík, 1998 (placed here tentatively based on general morphology; see Kovařík, 1998).
- Vachoniolus** Levy, Amitai et Shulov, 1973 (two species): **DM_c not visible:** *V. globimanus* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 43); *V. minipectenibus* (Levy, Amitai et Shulov, 1973) (Levy et al., 1973: Fig. 28, as *Buthacus*).
- Vachonus** Tikader et Bastawade, 1983 (two species): **DM_c visible:** *V. atrostriatus* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 501); *V. rajasthanicus* Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 488).
- Patellar trichobothrium d₃ external to carina DM_c**
- “**Ananteris group**”. **Trichobothrial pattern beta; femur trichobothrium d₂ located dorsally: (6 genera); tibial spur is lost in Akentrobuthus.**
- Akentrobuthus** Lamoral, 1976 (one species): **DM_c visible:** *A. leleupi* Lamoral, 1976 (Lamoral, 1976: Fig. 5).
- Ananteris** Thorell, 1891 (21 species): **DM_c visible:** *A. asmolei* Lourenço, 1981 (Lourenço, 1981: Fig. 24); *A. dekeyseri* Lourenço, 1982 (Lourenço, 1982b: Fig. 74); *A. evellynae* Lourenço, 2004 (Lourenço, 2004f: Fig. 3). **DM_c not visible:** *A. balzani* Thorell, 1891 (Lourenço, 1982b: Fig. 8; Lourenço, 2001g: Fig. 10); *A. charlescorfieldi* Lourenço, 2001 (Lourenço, 2001g: Fig. 8); *A. coineaui* Lourenço, 1982 (Lourenço, 1982b: Fig. 76); *A. cussinii* Borelli, 1910 (González-Sponga, 1996b: Fig. 276; Lourenço & Huber, 1999a: Fig. 4); *A. elisabethae* Lourenço, 2003 (Lourenço, 2003d: Fig. 19); *A. feae* (Borelli, 1911) (Lourenço, 1985: Fig. 16); *A. festae* Borelli, 1899 (Lourenço, 1982b: Fig. 78; Lourenço, 1999e: Fig. 8); *A. franckei* Lourenço, 1982 (Lourenço, 1982b: Fig. 72); *A. leilae* Lourenço, 1999 (Lourenço, 1999e: Fig. 4); *A. luciae* Lourenço, 1984 (Lourenço, 1984c: Fig. 4); *A. mariaelenae* Lourenço, 1999 (Lourenço, 1999f: Fig. 2); *A. mariaterzeae* Lourenço, 1982 (Lourenço, 1982b: Fig. 71); *A. mauryi* Lourenço, 1982 (Lourenço, 1982b: Fig. 73); *A. nairae* Lourenço, 2004 (Lourenço, 2004e: Fig. 8); *A. pydanieli* Lourenço, 1982 (Lourenço, 1982b: Fig. 75); *A. sabineae* Lourenço, 2001 (Lourenço, 2001g: Fig. 2F); *A. turumbanensis* González-Sponga, 1980 (González-Sponga, 1996b: Fig. 282); *A. venezuelensis* González-Sponga, 1982 (Lourenço, 1982b: Fig. 77; González-Sponga, 1996b: Fig. 279).
- Himalayotityobuthus** Lourenço, 1997 (one species): **DM_c visible:** *H. alejandrae* Lourenço, 2003 (Lourenço, 2003b: Fig. 12).
- Lychas** C. L. Koch, 1845 (14 species): **DM_c visible:** *L. albimanus* Henderson, 1919 (Tikader & Bastawade, 1983: Fig. 251); *L. biharensis* Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 267); *L. ceylonensis* Lourenço et Huber, 1999 (Lourenço & Huber, 1999b: Fig. 3); *L. flavimanus* (Thorell, 1888) (Vachon, 1986: Fig. 17); *L. hendersoni* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 180); *L. laevifrons* Pocock, 1897 (Tikader & Bastawade, 1983: Fig. 213); *L. mucronatus* (Fabricius, 1798) (Tikader & Bastawade, 1983: Fig. 150; **exception, d₃ internal to DM_c**); *L. nigristeris* (Pocock, 1899) (Tikader & Bastawade, 1983: Fig. 111);

L. rugosus (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 166: **exception**, d_3 internal to DM_c); *L. scaber* (Pocock, 1893) (Tikader & Bastawade, 1983, Fig. 235: **exception**, d_3 above DM_c); *L. sri-lankensis* Lourenço, 1997 (Lourenço, 1997f: Fig. 4; **exception**, d_3 internal to DM_c); *L. tricarinatus* (Simon, 1884) (Tikader & Bastawade, 1983: Fig. 197); *L. sp.* (Fig. 13, specimen examined, Singapore); *L. sp.* (specimen examined, Indonesia). **DM_c not visible:** *L. graveleyi* Henderson, 1913 (Tikader & Bastawade, 1983: Fig. 126); *L. kamshetensis* Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 282).

**Lychasioides* Vachon, 1974 (one species): *L. amieti* Vachon, 1974 (placed here since the genus is close to *Ananteris*; Lourenço, 1999j).

Microananteris* Lourenço, 2003 (one species): **DM_c not visible: *M. minor* Lourenço, 2003 (placed here since the genus is close to *Ananteris*; Lourenço, 2003a).

“Isometrus group”. Trichobothrial pattern *beta*; femur trichobothrium d_2 located internally, or on internal carina or absent (7 genera); tibial spur is lost in *Afroisometrus* and *Isometrus*

**Afroisometrus* Kovařík, 1997 (one species): *A. minshullae* (FitzPatrick, 1994) (Kovařík, 1997) (placement according to phylogeny of Prendini, 2004b).

Australobuthus Locket, 1990 (one species): **DM_c visible:** *A. xerolimnium* Locket, 1990 (Locket, 1990: Figs. 10B, 11A).

Babycurus Karsch, 1886 (six species): **DM_c visible:** *B. exquisitus* Lowe, 2000 (Lowe, 2000: Fig. 7); *B. jacksoni* (Pocock, 1890) (Vachon, 1940b: Fig. 14); *B. kirki* Pocock, 1890 (Vachon, 1940a: Fig. 13, as *Buthus*); *B. melanicus* Kovařík, 2000 (Prendini, 2004a: Fig. 7); *B. solegladi* Lourenço, 2005 (Lourenço, 2005a: Fig. 15); *B. zambonellii* Borelli, 1902 (Sissom, 1994: Fig. 4).

Hemilychas Hirst, 1911 (one species): **DM_c visible:** *H. alexandrinus* Hirst, 1911 (Locket, 1990: Fig. 11B, as *Lychas*; see also Kovařík, 1997a).

Isometroides Keyserling, 1885 (one species): **DM_c visible:** *I. vescus* (Karsch, 1880) (Locket, 1990: Fig. 11C; Lourenço, 2003b: Fig. 4; specimen examined).

Isometrus Ehrenberg, 1828 (18 species): **DM_c visible:** *I. acanthurus* Pocock, 1899 (Tikader & Bastawade, 1983: Fig. 877); *I. acanthurus loebli* Vachon, 1982 (Vachon, 1982: Fig. 60); *I. assamensis* Oates, 1888 (Tikader & Bastawade, 1983: Fig. 862); *I. basilicus* Karsch, 1879 (Vachon, 1982: Fig. 42); *I. besucheti* Vachon, 1982 (Vachon, 1982: Fig. 53); *I. brachycentrus* Pocock, 1899 (Tikader & Bastawade, 1983: Fig. 766); *I. corbeti* Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 893); *I. hain-*

anensis Lourenço, Qi et Zhu, 2005 (Lourenço et al., 2005a: Fig. 5); *I. heimi* Vachon, 1976 (Vachon, 1976: Fig. 5); *I. isadensis* Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 809); *I. kurkai* Kovařík, 1997 (Kovařík, 1997d: Fig. 4); *I. maculatus* (DeGeer, 1778) (Vachon, 1972: Figs. 3, 11; Tikader & Bastawade, 1983: Fig. 836, as *I. europaeus*; González-Sponga, 1996b: Fig. 295; Fig. 14, specimen examined); *Isometrus melanodactylus* (L. Koch, 1867) (specimen examined); *I. rigidulus* Pocock, 1897 (Tikader & Bastawade, 1983: Fig. 752); *I. thurstoni* Pocock, 1893 (Tikader & Bastawade, 1983: Fig. 794); *I. thwaitesi* Pocock, 1897 (Vachon, 1982: Fig. 30); *I. thwaitesi pallidus* Lourenço et Huber, 2002 (Lourenço & Huber, 2002: Fig. 4); *I. vittatus* Pocock, 1900 (Tikader & Bastawade, 1983: Fig. 736; **exception**, d_3 internal to DM_c); *I. zideki* Kovařík, 1994 (Kovařík, 1994: Fig. 3). **DM_c not visible:** *I. sankeriensis* Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 907).

**Odonturus* Karsch, 1879 (one species): *O. dentatus* Karsch, 1879 (placement according to phylogeny of Prendini, 2004b).

“Charmus group”. Trichobothrial pattern *alpha*; femur trichobothrium d_2 located dorsally (3 genera); tibial spurs present.

Charmus Karsch, 1879 (five species): **DM_c not visible:** *C. brignolii* Lourenço, 2000 (Lourenço, 2000e: Fig. 13); *C. indicus* Hirst, 1915 (Lourenço, 2000e: Fig. 7; Tikader & Bastawade, 1983: Fig. 392); *C. laneus* Karsch, 1879 (Vachon, 1982: Fig. 4); *C. minor* Lourenço, 2002 (Lourenço, 2002c: Fig. 13, 14); *C. sinhagadensis* Tikader & Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 412).

Somalicharmus Kovařík, 1998 (one species): **DM_c not visible:** *S. whitmanae* Kovařík, 1998 (Kovařík, 1998: Fig. 12).

Thaicharmus Kovařík, 1995 (one species): **DM_c not visible:** *T. mahunkai* Kovařík, 1995 (Kovařík, 1995: Fig. 10).

“Uroplectes group”. Trichobothrial pattern *alpha*; femur trichobothrium d_2 located internally or absent; (18 genera); tibial spurs present (Old World, including all three genera of Microcharmidae)

Ankaranocharmus Lourenço, 2004 (one species): **DM_c not visible:** *A. pauliani* Lourenço, 2004 (Lourenço, 2004a: Fig. 19) (currently under Microcharmidae); **femur trichobothrium d_2 absent** (placed here tentatively due to general morphology and biogeographic connections).

- Butheoloides** Hirst, 1925 (nine species): **DM_c visible:** *B. (Gigantoloides) aymerichi* Lourenço, 2002 (Lourenço, 2002e: Fig. 6), **exception, d₃ internal to DM_c.** **DM_c not visible:** *B. annieae* Lourenço, 1986 (Lourenço, 1986a: Fig. 16); *B. charlotteae* Lourenço, 2000 (Lourenço, 2000f: Fig. 5); *B. hirsti* Lourenço, 1996 (Lourenço, 1996b: Fig. 17); *B. maroccanus* Hirst, 1925 (Vachon, 1952: Fig. 129); *B. monodi* Vachon, 1950 (Vachon, 1950a: Fig. 2); *B. occidentalis* Lourenço, Slimani et Berahou, 2003 (Lourenço et al., 2003: Fig. 15); *B. polisi* Lourenço, 1996 (Lourenço, 1996b: Fig. 12); *B. schwendingeri* Lourenço, 2002 (Lourenço, 2002e: Fig. 8); *B. wilsoni* Lourenço, 1995 (Lourenço, 1995a: Fig. 4).
- Buthoscorpio** Werner, 1936 (two species): **DM_c not visible:** *B. politus* (Pocock, 1899) (Vachon, 1961: Fig. 1; Tikader & Bastawade, 1983: Fig. 427, as *Stenochirus*); *B. sarasinorum* (Karsch, 1891) (Vachon, 1982: Fig. 14, as *Stenochirus*; Tikader & Bastawade, 1983: Fig. 449, as *Stenochirus*).
- ***Egyptobuthus** Lourenço, 1999 (placed here since the genus is close to *Butheoloides*; Lourenço, 1999k).
- Grosphus** Simon, 1880 (12 species): **DM_c not visible:** *G. ankarafantsika* Lourenço, 2003 (Lourenço, 2003f: Fig. 14); *G. ankarana* Lourenço & Goodman, 2003 (Lourenço & Goodman, 2003b: Fig. 21); *G. darainensis* Lourenço, Goodman et Ramilijaona (Lourenço et al., 2004b: Fig. 7); *G. flavopiceus* Kraepelin, 1900 (Lourenço & Goodman, 2003b: Fig. 29); *G. garciai* Lourenço, 2001 (Lourenço, 2001j: Fig. 9); *G. griveaudi* Vachon, 1969 (Vachon, 1969: Fig. 2); *G. hirtus* Kraepelin, 1901 (Fig. 15, specimen examined); *G. intertidialis* Lourenço, 1999 (Lourenço, 1999h: Fig. 2); *G. madagascariensis* (Gervais, 1843) (specimen examined); *G. mahafaliensis* Lourenço, Goodman et Ramilijaona (Lourenço et al., 2004b: Fig. 3); *G. olgae* Lourenço, 2004 (Lourenço, 2004i: Fig. 3); *G. simoni* Lourenço, Goodman et Ramilijaona (Lourenço et al., 2004b: Fig. 11).
- Karasbergia** Hewitt, 1913 (one species): **DM_c visible:** *K. methueni* Hewitt, 1913 (Lamoral, 1979: Fig. 78); **femur trichobothrium d₂ absent.**
- Microcharmus** Lourenço, 1996 (one species): **DM_c visible:** *M. hauseri* Lourenço, 1996 (Lourenço, 1996c: Fig. 18, specimen examined, male holotype) (currently under Microcharmidae).
- Neogrosphus** Lourenço, 1995 (one species): **DM_c not visible:** *N. blanci* Lourenço, 1996 (Lourenço, 1996a: Fig. 23).
- Neoprotobuthus** Lourenço, 2000 (one species): **DM_c not visible:** *N. intermedius* Lourenço, 2000 (Lourenço, 2000a: Fig. 3 (currently under Microcharmidae).
- ***Palaeogrosphus** Lourenço, 2000 (placed here since the genus is close to *Grosphus*; Lourenço, 2000g).
- Parabuthus** Pocock, 1890 (17 species): **DM_c visible:** *P. gracilis* Lamoral, 1979 (Lamoral, 1979: Fig. 114); *P. granulatus* (Ehrenberg, 1828) (Lamoral, 1979: Fig. 121; specimen examined); *P. kraepelini* (Werner, 1902) (Lamoral, 1979: Fig. 137); *P. muelleri* Prendini, 2000 (Prendini, 2000: Fig. 4; Prendini, 2003: Fig. 10); *P. namibensis* Lamoral, 1979 (Lamoral, 1979: Fig. 161); *P. schlechteri* Purcell, 1899 (Lamoral, 1979: Fig. 185); *P. stridulus* Hewitt, 1913 (Lamoral, 1979: Fig. 195); *P. sp.* (Fig. 16, specimen examined). **DM_c not visible:** *P. brevismanus* (Thorell, 1877) (Lamoral, 1979: Fig. 91); *P. kalaharicus* Lamoral, 1977 (Lamoral, 1979: Fig. 130); *P. kraepelini* Werner, 1902 (Lamoral, 1979: Fig. 137); *P. kuanymarum* Monard, 1937 (Lamoral, 1979: Fig. 145); *P. laevifrons* (Simon, 1887) (Lamoral, 1979: Fig. 152); *P. liosoma* (Ehrenberg, 1829) (specimens examined); *P. pallidus* Pocock, 1895 (specimen examined); *P. raudus* (Simon, 1887) (Lamoral, 1979: Fig. 178); *P. transvaalicus* Purcell, 1899 (specimen examined); *P. villosus* (Peters, 1861) (Lamoral, 1979: Fig. 202).
- Pseudolissothus** Lourenço, 2001 (one species): **DM_c visible:** *P. pusillus* Lourenço, 2001 (Lourenço, 2001f: Fig. 2F).
- Pseudolychas** Kraepelin, 1911 (three species): **DM_c visible:** *P. ochraceus* (Hirst, 1911) (Prendini, 2004b: Fig. 20); *P. pegleri* (Purcell, 1901) (Prendini, 2004b: Fig. 31); *P. transvaalicus* Lawrence, 1961 (Prendini, 2004b: Fig. 42).
- ***Pseudouroplectes** Lourenço, 1995b (one species): *P. betschi* Lourenço, 1995 (placed here since the genus is close to *Uroplectes*; Lourenço, 1995b).
- Tityobuthus** Pocock, 1893 (12 species): **DM_c visible:** *T. baroni* (Pocock, 1890) (Lourenço, 1996a: Fig. 49); *T. lucileae* Lourenço, 1996 (Lourenço, 1996a: Fig. 53); *T. rakotondravonyi* Lourenço et Goodman, 2003 (Lourenço & Goodman, 2003a: Fig. 27). **DM_c not visible:** *T. antsingy* Lourenço et Goodman, 2004 (Lourenço & Goodman, 2004: Fig. 4); *T. darainensis* Lourenço et Goodman, 2002 (Lourenço & Goodman, 2002: Fig. 52). *T. dastychi* Lourenço, 1997 (Lourenço, 1997b: Fig. 5); *T. griswoldi* Lourenço, 2000 (Lourenço, 2000g: Fig. 20); *T. ivohibe* Lourenço et Goodman, 1999 (Lourenço & Goodman, 1999: Fig. 8); *T. manonae* Lourenço, 2000 (Lourenço, 2000g: Fig. 16); *T. monodi* Lourenço, 2000 (Lourenço, 2000g: Fig. 25); *T. pallidus* Lourenço, 2004 (Lourenço, 2004h: Fig. 2B); *T. pococki* Lourenço, 1995 (Lourenço, 1995a: Fig. 19).
- Troglotityobuthus** Lourenço, 2000 (one species): **DM_c visible:** *T. gracilis* (Fage, 1946) (Lourenço, 2000g: Fig. 7).
- Uroplectes** Peters, 1861 (11 species): **DM_c visible:** *U. gracilior* Hewitt, 1913 (Lamoral, 1979: Fig. 240);

U. longimanus Werner, 1936 (Lamoral, 1979: Fig. 247); *U. occidentalis* Simon, 1876 (Vachon, 1950b: Fig. 12; Lourenço, 2000h: Fig. 2D); *U. vittatus* (Thorell, 1876) (Fig. 17, specimen examined; specimen examined, traces of DM_c visible). **DM_c not visible:** *U. carinatus* (Pocock, 1890) (Lamoral, 1979: Fig. 213); *U. otjimbinguensis* (Karsch, 1879) (Lamoral, 1979: Fig. 256); *U. pilosus* (Thorell, 1876) (Lamoral, 1979: Fig. 264); *U. planimanus* (Karsch, 1879) (Lamoral, 1979: Fig. 272; specimen examined); *U. schlechteri* Purcell, 1901 (Lamoral, 1979: Fig. 280); *U. teretipes* Lawrence, 1966 (Lamoral, 1979: Fig. 287); *U. tumidimanus* Lamoral, 1979 (Lamoral, 1979: Fig. 295).

Uroplectoides Lourenço, 1998 (one species): **DM_c not visible:** *U. abyssinicus* Lourenço, 1998 (Lourenço, 1998c: Fig. 3).

“Tityus group”. Trichobothrial pattern α ; femur trichobothrium d_2 located internally or absent (9 genera); tibial spurs absent (New World)

Alayotityus Armas, 1973; **femur trichobothrium d_2 absent** (placed here due to general morphology and biogeographic connections) (five species): **DM_c visible:** *A. delacruzii* Armas, 1973 (Vachon, 1977: Fig. 1; Teruel, 2001a: Fig. 3); *A. granma* Armas, 1984 (Armas, 1984: Fig. 3C); *A. juraguaensis* Armas, 1973 (Armas, 1973: Fig. 9); *A. nanus* Armas, 1973 (Fig. 21, specimen examined); *A. sierramaestrae* Armas, 1979 (Lourenço & Vachon, 1996: Fig. 10; Lourenço, 1999b: Fig. 15).

Centruroides Marx, 1890 (34 species): **DM_c visible:** *C. barbudensis* (Pocock, 1898) (Armas, 1983: Fig. 17A, 24A as *C. hummelincki*; Lourenço, 1984b: Fig. 10); *C. bicolor* (Pocock, 1898) (Francke & Stockwell, 1987: Fig. 17), specimen examined; *C. elegans* (Thorell, 1876), (specimen examined); *C. exilicauda* (Wood, 1863), (specimen examined); *C. exilimanus* Teruel et Stockwell, 2002 (Teruel & Stockwell, 2002: Fig. 14); *C. exsul* (Meise, 1934) (Sissom & Lourenço, 1987: Fig. 35); *C. gracilis* (Latreille, 1804) (Sissom & Lourenço, 1987: Fig. 6; González-Sponga, 1996b: Fig. 287); *C. griseus* (C. L. Koch, 1844) (Francke & Sissom, 1980: Fig. 32; Armas, 1982: Fig. 4B, as *C. g. borinquensis*); *C. hasethi* Pocock, 1902 (González-Sponga, 1996b: Fig. 290); *C. hentzi* (Banks, 1910), (specimen examined); *C. hoffmanni* Armas, 1996 (Armas, 1996: Fig. 6); *C. infamatus ornatus* Pocock, 1902, (specimen examined); *C. koesteri* Kraepelin, 1911 (Francke & Stockwell, 1987: Fig. 26; specimen examined); *C. limbatus* (Pocock, 1898) (Francke & Stockwell, 1987: Fig. 37; specimen examined); *C. limpidus* (Karsch, 1879), specimen examined; *C. lu-*

ceorum Armas, 1999 (Armas, 1999: Fig. 9C); *C. mahnerti* Lourenço, 1983 (Lourenço, 1983b: Fig. 9); *C. margaritatus* (Gervais, 1841) (Fig. 18, specimen examined; Francke & Stockwell, 1987: Fig. 46; Sissom & Lourenço, 1987: Figs. 19, 25); *C. melanodactylus* Teruel, 2001 (Teruel, 2001b: Fig. 11); *C. navarroii* Teruel, 2001 (Teruel, 2001b: Fig. 3); *C. nigrescens* (Pocock, 1898), specimen examined; *C. nigrovariatus baergi* Hoffmann, 1932, (specimen examined); *C. nitidus* (Thorell, 1877) (Schawaller, 1979: Fig. 6; as *C. beynai*, a fossil species from Dominican amber); *C. noxius* Hoffmann, 1932, (specimen examined); *C. pallidiceps* Pocock, 1902, (specimen examined); *C. pococki* Sissom et Francke, 1983 (Sissom & Francke, 1983: Fig. 5); *C. rileyi* Sissom, 1995 (Sissom, 1995: Fig. 23); *C. schmidtii* Sissom, 1995 (Sissom, 1995: Fig. 14); *C. sculpturatus* Ewing, 1928, (specimen examined); *C. sissomi* Armas, 1996 (Armas, 1996: Fig. 2); *C. stockwelli* Teruel, 2001 (Teruel, 2001b: Fig. 22); *C. testaceus* (DeGeer, 1778) (Sissom & Francke, 1983: Fig. 17); *C. thorelli* Kraepelin, 1891 (Francke & Stockwell, 1987: Fig. 55; Sissom, 1995: Fig. 5); *C. vittatus* (Say, 1821), (specimen examined).

Mesotityus González-Sponga, 1981 (one species): **DM_c visible:** *M. vondangeli* González-Sponga, 1981 (González-Sponga, 1981: Fig. 2; González-Sponga, 1996b: Fig. 301).

Microtityus Kjellesvig-Waering, 1966 (nine species): **DM_c visible:** *M. ambarensis* (Schawaller, 1981) (Schawaller, 1981: Fig. 9; a fossil species from Dominican amber, as *Tityus ambarensis*); *M. biordi* González-Sponga, 1970 (González-Sponga, 1996b: Fig. 308); *M. dominicanensis* Santiago-Blay, 1985 (Santiago-Blay, 1985a: Fig. 6); *M. farleyi* Teruel, 2000 (Teruel, 2000: Fig. 2); *M. guantanamo* Armas, 1984 (Armas, 1984: Fig. 6B); *M. joseantonioi* González-Sponga, 1981 (González-Sponga, 1981: Fig. 11; González-Sponga, 1996b: Fig. 311); *M. starri* Lourenço et Huber, 1999 (Lourenço & Huber, 1999a: Fig. 17); *M. vanzolinii* Lourenço et Von Eickstedt, 1983 (Lourenço & Von Eickstedt, 1983b: Fig. 6); *M. waeringi* Francke et Sissom, 1980 (Francke & Sissom, 1980: Fig. 24).

Rhopalurus Thorell, 1876 (two species): **DM_c visible:** *R. junceus* (Herbst, 1800) (Fig. 20, specimen examined); *R. laticauda* Thorell, 1876 (González-Sponga, 1996b: Fig. 317).

Tityopsis Armas, 1974 (two species): **DM_c visible:** *T. aliciae* Armas et Martín Frías, 1998 (Armas & Martín Frías, 1998: Fig. 1B); *T. inaequalis* (Armas, 1974) (Lourenço & Vachon, 1996: Fig. 16).

Tityus C. L. Koch, 1836 (90 species): **DM_c visible:** *T. adisi* Lourenço et Pézier, 2002 (Lourenço & Pézier, 2002: Fig. 14); *T. adrianoi* Lourenço, 2003 (Lourenço, 2003g: Fig. 5); *T. anaeae* Lourenço, 1997

- (Lourenço, 1997a: Fig. 5); *T. antioquiensis* Lourenço et Otero Patino, 1998 (Lourenço & Otero Patino, 1998: Figs. 2, 4); *T. apiacas* Lourenço, 2002 (Lourenço, 2002d: Figs. 2, 7); *T. arellanoparra* González-Sponga, 1985 (González-Sponga, 1996b: Fig. 330); *T. bahiensis* (Perty, 1833) (Lourenço, 1982d: Fig. 9); *T. bahiensis eickstedtae* Lourenço, 1982 (Lourenço, 1982d: Fig. 6, as *T. eickstedtae*); *T. barquisimetus* González-Sponga, 1994 (González-Sponga, 1996b: Fig. 407); *T. betschi* Lourenço, 1992 (Lourenço, 1992: Fig. 2); *T. blaseri* Mello-Leitão, 1931 (Lourenço et al., 1997: Fig. 3); *T. boconoensis* González-Sponga, 1981 (González-Sponga, 1996b: Fig. 395); *T. braziliae* Lourenço et Von Eickstedt, 1984 (Lourenço & Von Eickstedt, 1984: Figs. 4, 11); *T. canopenis* Lourenço et Pézier, 2002 (Lourenço & Pézier, 2002a: Fig. 1); *T. carabobensis* González-Sponga, 1987 (González-Sponga, 1996b: Fig. 403). *T. cerroazul* Lourenço, 1986 (Lourenço, 1986b: Fig. 4); *T. championi* Pocock, 1898 (Francke & Stockwell, 1987: Fig. 69; specimen examined); *T. charreyroni* Vellard, 1932 (Lourenço, 1980b: Fig. 28, as *T. trivittatus charreyroni*; Lourenço, 2001i: Fig. 9); *T. clathratus* C. L. Koch, 1844 (Lourenço, 1983a: Fig. 21; González-Sponga, 1996b: Fig. 357); *T. columbianus* (Thorell, 1876) (Lourenço, 1981: Fig. 7); *T. confluens* Borelli, 1899 (Lourenço, 1980: Fig. 40); *T. costatus* (Karsch, 1879) (Lourenço, 1980b: Fig. 22, as *T. trivittatus dorsomaculatus*; Lourenço & Giupponi, 2004: Figs. 5, 10); *T. culebrensis* González-Sponga, 1994 (González-Sponga, 1996b: Fig. 411); *T. dasyurus* Pocock, 1897 (Lourenço & Francke, 1984: Fig. 6; Santiago-Blay, 1985b: Fig. 5); *T. dedoslargos* Francke et Stockwell, 1987 (Francke & Stockwell, 1987: Fig. 78; specimen examined); *T. demangei* Lourenço, 1981 (Lourenço, 1981: Fig. 15); *T. dinizi* Lourenço, 1997 (Lourenço, 1997e: Fig. 5); *T. discrepans* (Karsch, 1879) (González-Sponga, 1996b: Fig. 324); *T. dupouyi* González-Sponga, 1987 (González-Sponga, 1996b: Fig. 348); *T. ecuadorensis* Kraepelin, 1896 (Lourenço, 1983c: Fig. 5; specimen examined); *T. elizabethae* Lourenço et Ramos, 2004 (Lourenço & Ramos, 2004: Fig. 13); *T. erikae* Lourenço, 1999 (Lourenço, 1999i: Fig. 3); *T. exstinctus* Lourenço, 1995 (Lourenço, 1995: Fig. 3); *T. falconensis* González-Sponga, 1974 (González-Sponga, 1996b: Fig. 383); *T. fasciolatus* Pessôa, 1935 (Lourenço, 1980b: Fig. 34, as *T. trivittatus fasciolatus*); *T. filodendron* González-Sponga, 1981 (González-Sponga, 1996b: Fig. 339); *T. florezi* Lourenço, 2000 (Lourenço, 2000d: Fig. 9); *T. fuhrmani* Kraepelin, 1914 (Lourenço, 1984a: Fig. 7); *T. funestus* Hirst, 1911 (González-Sponga, 1996b: Fig. 371); *T. gaffini* Lourenço, 2000 (Lourenço, 2000d: Fig. 2); *T. geratus* Santiago-Blay et Poinar, 1988 (Santiago-Blay & Poinar, 1988: Fig. 4; a fossil species from Dominican amber); *T. gasci* Lourenço, 1982 (Lourenço, 1982a: Fig. 5); *T. gonzalezspingai* Quiroga, De Sousa, Parrilla-Álvarez et Manzanilla: Quiroga et al., 2004: Figs. 3.2, 6.2); *T. insignis* (Pocock, 1889) (Lourenço, 1984e: Fig. 6, 16); *T. jeanvelliardi* Lourenço, 2001 (Lourenço, 2001i: Fig. 26); *T. kuryi* Lourenço, 1997 (Lourenço, 1997c: Fig. 3); *T. lancinii* González-Sponga, 1972 (González-Sponga, 1996b: Fig. 379); *T. magnimanus* Pocock, 1897 (Lourenço, 1987: Fig. 8); *T. martinpaechi* Lourenço, 2001 (Lourenço, 2001e: Fig. 10); *T. mathieseni* Rocha et Lourenço, 2000 (Rocha & Lourenço, 2000: Fig. 5); *T. melanostictus* Pocock, 1893 (González-Sponga, 1996b: Fig. 360); *T. melici* Lourenço, 2003 (Lourenço, 2003c: Fig. 4); *T. meridanus* González-Sponga, 1981 (González-Sponga, 1996b: Fig. 342); *T. metuendus* Pocock, 1897 (Lourenço, 1983d: Fig. 6); *T. monaguensis* González-Sponga, 1974 (González-Sponga, 1996b: Fig. 387); *T. munozi* Lourenço, 1997 (Lourenço, 1997c: Fig. 10); *T. nematochirus* Mello-Leitão, 1940 (Fig. 20, specimen examined; González-Sponga, 1996a: Figs. 79, 83; González-Sponga, 1996b: Fig. 333); *T. neoespartanus* González-Sponga, 1996 (González-Sponga, 1996a: Figs. 1, 7); *T. nororientalis* González-Sponga, 1996 (González-Sponga, 1996a: Figs. 11, 17); *T. obtusus* (Karsch, 1879) (Armas, 1977: Fig. 1C); *T. ocelote* Francke et Stockwell, 1987 (Francke & Stockwell, 1987: Fig. 87; specimen examined); *T. osmanus* González-Sponga, 1996 (González-Sponga, 1996a: Figs. 22, 25); *T. pachyurus* Pocock, 1897 (Lourenço & Méndez, 1984: Fig. 6; Francke & Stockwell, 1987: Fig. 94); *T. paraensis* Kraepelin, 1896 (Lourenço, 1983a: Figs. 7, 13, as *T. cambridgei*); *T. parvulus* Kraepelin, 1914 (Lourenço, 1999g: Fig. 2); *T. perijanensis* González-Sponga, 1994 (González-Sponga, 1996b: Fig. 351); *T. pictus* Pocock, 1893 (Lourenço, 1984e: Fig. 24); *T. pittieri* González-Sponga, 1981 (González-Sponga, 1996b: Fig. 327); *T. pococki* Hirst, 1907 (Lourenço, 1987: Fig. 19; González-Sponga, 1996a: Figs. 59, 64; González-Sponga, 1996b: Fig. 363); *T. potameis* Lourenço et Giupponi, 2004 (Lourenço & Giupponi, 2004: Figs. 22, 25); *T. prancei* Lourenço, 2000 (Lourenço, 2000d: Fig. 6); *T. pugilator* Pocock, 1898 (Lourenço, 1980a: Fig. 7, as *T. kraepelini*); *T. pusillus* Pocock, 1893 (Lourenço, 1982c: Fig. 5); *T. rebierei* Lourenço, 1997 (Lourenço, 1997d: Fig. 37); *T. riocaurensis* González-Sponga, 1996 (González-Sponga, 1996a: Figs. 29, 35); *T. roigi* Maury et Lourenço, 1987 (Maury & Lourenço, 1987: Fig. 4); *T. rojasi* González-Sponga, 1996 (González-Sponga, 1996a: Figs. 39, 45); *T. rugosus* Schenkel, 1932 (González-Sponga, 1996a: Figs. 69, 74; González-Sponga, 1996b: Fig. 367); *T. serrula-*

tus Lutz et Mello, 1922 (Lourenço & Von Eickstedt, 1983a: Fig. 5); *T. shiriana* González-Sponga, 1991 (González-Sponga, 1996b: Fig. 354); *T. silvestris* Pocock, 1897 (Lourenço, 1983a: Fig. 28); *T. suro-orientalis* González-Sponga, 1996 (González-Sponga, 1996a: Figs. 49, 55); *T. tamayoi* González-Sponga, 1987 (González-Sponga, 1996b: Fig. 345); *T. trinitatis* Pocock, 1897 (Lourenço, 1984d: Fig. 3); *T. trivittatus* Kraepelin, 1898 (Lourenço, 1980b: Fig. 16); *T. unus* Pinto-da-Rocha et Lourenço, 2000 (Pinto-da-Rocha & Lourenço, 2000: Fig. 15); *T. urbinai* Scorza, 1952 (González-Sponga, 1996b: Fig. 336); *T. vaissadei* Lourenço, 2002 (Lourenço, 2002d: Fig. 18); *T. valerae* Scorza, 1954 (González-Sponga, 1996b: Fig. 375); *T. venamensis* González-Sponga, 1981 (González-Sponga, 1996b: Fig. 399). *T. zulianus* González-Sponga, 1981 (González-Sponga, 1996b: Fig. 391). **DM_c not visible:** *T. otero-i* Lourenço, 1998 (Lourenço, 1998d: Figs. 2D, 3D).

Troglophalurus Lourenço, Baptista et Giupponi, 2004 (one species): **DM_c visible:** *T. translucidus* Lourenço, Baptista et Giupponi, 2004 (Lourenço et al., 2004a: Fig. 8).

Zabius Thorell, 1893; **femur trichobothrium d_2 absent** (placed here due to general morphology and biogeographic connections) (three species): **DM_c visible:** *Z. birabeni* Mello-Leitão, 1938; *Z. fuscus* (Thorell, 1876); *Z. sp.n.* (L. Acosta, pers. comm.).

Exceptions

Although it is not our goal to evaluate the accuracy and/or artistic value of the figures examined in literature for this study, it is clear some scorpologists produced more exact and accurate figures than others, and, in some cases, these renderings over the years are not consistent for an author. Consequently, we have factored in our own unstated subjective opinions into the evaluation of these stated exceptions. We address each exception noted above by group and genus:

Buthus group. 39 genera and 113 species, one exception: ***Buthacus***. *B. zieglerei*, in Lourenço's (2000c: Fig. 6) figure, d_3 is depicted external to DM_c .

Ananteris group. Six genera and 39 species, four exceptions. ***Lychas***: *L. mucronatus*: for this species, in Tikader & Bastawade's (1983: Fig. 150) figure trichobothria d_1 – d_5 are depicted quite high on the segment, all, including d_4 , positioned internal to the DM_c carina. We find this configuration highly unlikely, especially the position of trichobothrium d_4 and therefore dismiss it from consideration. *L. rugosus*: in Tikader & Bastawade's (1983: Fig. 166) we note that trichobothrium d_4 is depicted external to the DM_c carina and therefore cannot object to the figure on its surface value; *L. scaber*: in Tikader & Bastawade's (1983, Fig. 235)

figure both the d_3 and d_4 trichobothria are depicted as positioned internal to the DM_c carina, we, again, dismiss this discrepancy due to the position of d_4 . *L. srilankensis*: in Lourenço's (1997f: Fig. 4) figure, d_3 is depicted internal to DM_c .

Isometrus* group.** Seven genera and 29 species, one exception. ***Isometrus: *I. vittatus*: in Tikader & Bastawade's (1983: Fig. 736) figure, trichobothria d_1 and d_2 are depicted internal to the dorsointernal (DI_c) carina and both d_3 and d_4 internal to the DM_c carina, clearly an unlikely configuration, and therefore, we dismiss this as an exception.

***Charmus* group.** Three genera and 7 species, no exceptions.

Uroplectes* group.** 18 genera and 76 species, one exception: ***Butheoloides. *B. (Gigantoloides) aymerichi* in Lourenço's (2002e: Fig. 6) figure, d_3 is depicted internal to an apparent DM_c carina. From the figure we see that trichobothrium d_3 is placed external to d_1 and d_4 , a typical alignment for this genus. The problem with the figure is the depiction of the DM_c carina which bends considerably in an external direction at midsegment, almost reaching the DE_c carina. Clearly this area of the "carina" must be extraneous granulation and therefore we dismiss it as an accurate depiction.

***Tityus* group.** Nine genera and 143 species, no exceptions.

In summary, out of seven stated exceptions we are left with three which we accept as plausible based solely on the figure as illustrated. This accounts for less than 1 % of the data gathered.

Fossil buthoids (6 genera)

***Palaeolychas balticus* Lourenço et Weitschat, 1996 (Lourenço & Weitschat, 1996: Fig. 5).** Authors state: "tibia and chelae feebly carinate; all faces feebly granular". Our analysis based on figure and text: DM_c presence unknown; *beta* pattern, d_2 not shown, not known if it is absent, undetected or has migrated to internal surface (which shows three trichobothria); 4–5 dorsal trichobothria shown on patella, d_3 positioned slightly towards external edge, somewhat external to segment midpoint; tibial spur present.

Assuming femoral trichobothrial d_2 has migrated to internal surface and considering the somewhat external position of patellar trichobothria d_3 , we can tentatively place this fossil scorpion in the ***Isometrus*** group.

***Palaeotityobuthus longiaculeus* Lourenço et Weitschat, 2000.** Femur and patella unknown; tibial spur absent.

***Palaeoprotobuthus pusillus* Lourenço et Weitschat, 2000.** Authors state: "Patella feebly carinate". DM_c presence unknown; only one trichobothrium detectable on femur and four on patella, thus *alpha/beta*

pattern or patellar d_3 position unknown; tibial spur absent.

Palaeoakentrobuthus knodeli Lourenço et Weitschat, 2000 (Lourenço & Weitschat, 2000: Fig. 10). Authors state “tibia with five keels: one internal, 3 dorsal and 1 external”. We assume here the referenced carinae are DPS_c , DI_c , DM_c , DE_c , and EM_c which are typically visible in Recent buthoids if the patella is viewed dorsally; α pattern with d_2 apparently occurring on the dorsal surface; patellar trichobothrium d_3 positioned on external half of segment; tibial spur present.

Assuming femoral trichobothrial d_2 is located on dorsal surface and considering the somewhat external position of patellar trichobothria d_3 , this fossil scorpion can be tentatively placed in the *Charmus* group.

Palaeoananteris ribnitiodamgartensis Lourenço et Weitschat, 2001 (Lourenço & Weitschat, 2001: Fig. 2c). Authors state “tibia with 7 keels”; the figure shows the patella with a granulate carina with trichobothrium d_3 situated slightly internal and d_4 external. Based on the relative positions of the five dorsal trichobothria, we must assume the carina shown is DM_c ; femur reported with four dorsal trichobothria, d_2 either undetected, absent, or positioned on internal surface, α pattern depicted; tibial spurs present.

Assuming Fig. 2c is correct and assumptions stated above are true, this is the only example of a buthoid with an α pattern and trichobothrium d_3 positioned internal to the DM_c carina. Therefore, this fossil cannot be placed in any of the six hypothesized Recent buthoid groups.

Uintascorpio Perry, 1995: DM_c carina visible (Santiago-Blay et al. 2004b: Fig. 5); trichobothria not visible nor the presence or absence of the tibial spurs is determinable.

Cladistic Analysis

In this analysis we were interested primarily to see the effect of the new d_3 - DM_c alignment character as it related to the expanded α/β definition as originally defined by Soleglad & Fet (2003b). It was very clear in Soleglad & Fet’s (2003b) recent analysis of the α/β pattern, which incorporated other primitive Recent scorpions and fossils, that this pattern was important phylogenetically in the upper-level analysis of the buthoids. It is obvious that Vachon (1975) also realized the importance of the α/β pattern when he correlated all known buthoid genera and their biogeography with the α/β pattern.

In an attempt to isolate other basic buthoid characters, using Sissom’s (1990) key to buthoid genera as a basis, we decided to include the leg tibial spurs as well. The only other character used in the key that occurred in

several places was the “shape of the sternum”. However, based on the recent analysis of Soleglad & Fet (2003a), it is clear that the sternum “shape” is a bogus character and does not provide any meaningful phylogenetic information.

Use of generic names as terminal tokens. We need to stress here that the use of generic names as terminal taxa in the cladograms presented in this analysis, and analyses in previous publications for that matter (e.g., Soleglad & Fet, 2003b, etc.) does not necessarily imply monophyly of these genera. This should be particularly clear when, as in the case referenced above, the actual species set used for the cladistic analysis of that genus is *specifically stated*, and in many cases only one or two species were considered. It is clear that monophyly for a given genus can *only* be demonstrated if and only if a competent detailed species-level cladistic analysis is conducted which includes all species defined under that genus and select individuals from all immediate putative sister genera are included as outgroups; as for example, recently presented in Prendini’s (2004b) impressive analysis of genus *Pseudolychas* which included all three species. Therefore, we emphasize here that the use of no less than 82 generic names in our cladograms in this paper certainly does not state or even imply that they are monophyletic.

Character definitions

This analysis is based on six characters: two involving the pedipalp patella — the existence of the patellar DM_c carina, and the arrangement of trichobothrium d_3 and carina DM_c ; three concerning the pedipalp femur — the angles formed by femoral trichobothria d_1 - d_3 and d_3 - d_4 , and the surface orientation of trichobothrium d_2 ; and one involving the leg, the existence or absence of tibial spurs (legs III-IV or IV).

Note: for this study, we ignore the parallel alignment of femoral trichobothria d_1 - d_3 - d_4 exhibited in genus *Liobuthus*, as well as the occasional absent and/or vestigial state of trichobothrium d_2 in other species. Clearly, these derivations are autapomorphic to these taxa and therefore do not affect the overall results presented in this paper.

Character 1: Existence of the pedipalp patella dorso-medial (DM_c) carina (*unordered*)

0: carina absent (*Archaeobuthus*, *Pseudochactas*)

1: carina present (all buthoids)

This character is included for two reasons: One, the character represents a synapomorphy for parvorder Buthida (or superfamily Buthoidea), as originally established by Soleglad & Fet (2003b), and two, it is directly relevant to the definition of character-2 below, the subject of this paper.

Character 2: Alignment of patella trichobothrium d_3 with respect to the DM_c carina (*unordered*)

0: d_3 external to DM_c (*Ananteris*, *Isometrus*, *Charmus*, *Uroplectes*, and *Tityus* groups)

1: d_3 internal to DM_c (*Buthus* group)

(-): (*Archaeobuthus*, *Pseudochactas*)

As discussed below, we test four possible combinations of assigned polarity for this character using outgroup genus *Pseudochactas*. The result based on the state assignment of inapplicable (-) best represents, in our opinion, the most likely topology of the six hypothesized buthoid groups (Fig. 23). Different arguments for hypothesizing the plesiomorphic state of this character for the buthoids based on *Pseudochactas* are essentially equivocal. First, the DM_c carina does not exist in *Pseudochactas* and therefore, determining the position of trichobothrium d_3 with respect to a non-existent carina can certainly be termed inapplicable in a cladistic sense. On the other hand, one could argue that, since the DM_c carina clearly evolved after the formation of the orthobothriotaxic trichobothria in common to these two parvorders (Pseudochactida and Buthida), we can determine polarity based on the position of d_3 on the segment in *Pseudochactas*, presumably more primitive than the buthoids. In Fig. 3, we see d_3 located on the external half (i.e., towards the DE_c carina) of the patellar dorsal surface in this genus. From this we could conclude that “ d_3 external to DM_c ” is the most likely primitive state for the buthoids. However, one may argue also that we do not know what the effect of the derivation of a new carina has on the surface topology of the patella, maybe obscuring any localized positioning of a trichobothrium. In addition, one may argue that the trichobothria homology between the buthoids and *Pseudochactas* established by Soleglad & Fet (2001) is incorrect; that is, what we term as d_3 across the two parvorders may not, in fact, be the same trichobothrium (i.e., originating from a single derivation). Arguments for state assignment “unknown” (?) can be given along the same lines as that presented for inapplicable (-) and, probably the least likely assignment, “ d_3 internal to DM_c ”, cannot be reasonably defended at all—we have no DM_c carina for reference and d_3 is not located on the internal half (i.e., not closer to the DI_c carina) in *Pseudochactas*.

Character 3: Orientation of femoral trichobothria d_1 – d_3 with respect to dorsal carinae (*ordered*)

0: parallel (*Archaeobuthus*)

1: d_1 – d_3 angle towards the dorsoexternal carina (*beta*) (*Pseudochactas*, *Buthus*, *Ananteris*, and *Isometrus* groups)

2: d_1 – d_3 angle towards the dorsointernal carina (*alpha*) (*Charmus*, *Uroplectes*, and *Tityus* groups)

This character represents one-half of the *alpha/beta* pattern and demonstrates the intermediate position of *Pseudochactas* between the fossil *Archaeobuthus* and the buthoids when combined with character-4. For this character *Pseudochactas* agrees with the *beta* pattern of the buthoids.

Character 4: Orientation of femoral trichobothria d_3 – d_4 with respect to dorsal carinae (*ordered*)

0: parallel (*Archaeobuthus*, *Pseudochactas*)

1: d_3 – d_4 angle towards the dorsointernal carina (*beta*) (*Buthus*, *Ananteris*, and *Isometrus* groups)

2: d_3 – d_4 angle towards the dorsoexternal carina (*alpha*) (*Charmus*, *Uroplectes*, and *Tityus* groups)

For this character we see the primitive nature of *Pseudochactas*, complying with *Archaeobuthus*, thus showing that *Pseudochactas* is intermediate between *Archaeobuthus* and the buthoids (see character-3).

Character 5: Position of femoral trichobothrium d_2 (*unordered*)

0: located on dorsal surface (*Archaeobuthus*, *Pseudochactas*, *Buthus*, *Ananteris*, and *Charmus* groups)

1: located on internal surface or dorsointernal carina (*Isometrus*, *Uroplectes*, and *Tityus* groups)

By simple inspection we can see that this character is incongruent with characters 3 and 4 (refer to Table 1). This incongruency is demonstrated in all four cladograms depicted in Figs. 23–25. We opted to model this character with a single derivation although it is clear that the migration of femoral trichobothrium d_2 to the internal surface occurred separately in two clades, *Isometrus* group and *Uroplectes* + *Tityus* groups. For the former, based on available data, we detected a tendency of d_2 occurring on the dorsointernal carina, implying, in a sense, a lesser dislocation of the trichobothrium. This slight distinction could provide rationale for two character states.

Character 6: Tibial spurs of legs (III–IV or IV) (*unordered*)

0: spur present or sometimes vestigial (*Pseudochactas*, *Charmus* and *Uroplectes* groups, and most genera of *Buthus*, *Ananteris*, and *Isometrus* groups)

1: spur absent (*Archaeobuthus*)

2: spur absent (*Buthus* group: *Lanzatus*, *Liobuthus*, *Pectinibuthus*, *Plesiobuthus*, *Sabinebuthus*, *Vachonibuthus*)

3: spur absent (*Ananteris* group: *Akentrobuthus*)

4: spur absent (*Isometrus* group: *Isometrus*, *Afroisometrus*)

5: spur absent (*Tityus* group)

This somewhat irregular character, from a cladistic perspective, is included because we believe it is significant phylogenetically for the New World *Tityus* group, for reasons discussed elsewhere. Other occurrences, modeled as separate state derivations, are considered less important phylogenetically, many possibly the byproduct of specialized microhabitat adaptation. As suggested recently in Soleglad et al. (2005), the use of separate state values for similar looking derivations is a weaker assumption than assuming all such character changes occurred as a single derivation, and we adopt this approach here. Not only is it a weaker assumption, but equally as important, we do not believe these 19 occurrences of tibial spur losses are the product of a single evolutionary event and therefore, model these character states in accordance with the results based on the other characters. The presumed primitive state, tibial spurs being present, is based on their presence in many fossils, as well as in the most primitive Recent scorpion *Pseudochactas*.

Character ordering

Characters 3 and 4, which define the angle direction of femoral trichobothria d_1-d_3 and d_3-d_4 with respect to the dorsal carinae, are ordered in this analysis. We ordered these two characters because we believe they do reflect the true evolution of the *alpha/beta* pattern which they represent (i.e., as they are distributed in the cladograms presented in Figs. 23–25). This belief is based on solid polarity information provided by the outgroup taxa, the fossil *Archaeobuthus* and the primitive Recent scorpion *Pseudochactas*: (1) *Pseudochactas* is intermediate between *Archaeobuthus* and the buthoids by exhibiting only “one-half” of the *beta* pattern (character-3), while being consistent with *Archaeobuthus* in character-4; and, (2) this is further supported by the dorsal placement of trichobothrium d_2 in the two outgroup taxa, a *beta* pattern characteristic. In addition, these two characters exhibit congruency with the patella d_3-DM_c character (character-2) described in detail in this paper. In Soleglad & Fet (2003b), these two characters were not ordered.

We might add here that we obtain the same topology as shown in Figs. 23–25 and overall tree support data when these characters are not ordered. The only differences in the four combinations of character-2 assignment to *Pseudochactas* (see Table 2) is the number of resulting MPTs: ten MPTs instead of nine for inapplicable (-) and unknown (?) assignments, and four MPTs instead of three for “ d_3 external to DM_c ” assignment. The percentage of tree support for majority-rule consensus is essentially the same for these different MPT counts, 67 % being replaced with 60–70 % in the ten MPT case and 67 % being replaced with 75 % in the four MPT case.

Results

We exercised four separate cladistic sequences spanning all possible combinations of hypothesized polarity for the new character, d_3-DM_c (character-2). In particular, we used the outgroup genus *Pseudochactas* as a vehicle for assigning polarity of this character to the buthoids. As discussed above, this approach is necessary because neither of the two outgroups exhibit the DM_c carina and therefore one cannot establish its polarity with any certainty. Plausible arguments supporting each one of these assignments are presented above under the description of this character.

Figure 23 presents the topology and a complete detailed breakdown of all buthoid genera for the case where character-2 is assigned an inapplicable (-) state value to *Pseudochactas*. We used the topology presented in this cladogram as the basis for the groups of genera proposed in this paper. It is important to note here that two of these groups, the *Ananteris* group and the *Uroplectes* group, are not supported as monophyletic groups; that is, this limited character set does not provide any synapomorphies for these clades. The other four groups are supported by at least two-thirds of the trees (six out of nine): the parvorder Buthida (or superfamily Buthoidea) is supported by all trees, two of the characters providing unambiguous synapomorphies, character-1 (state = 1), derivation of the DM_c carina, and character-4 (state = 1), completion of the *beta* pattern. Clade (*Charmus* group + *Uroplectes* group + *Tityus* group) is also supported by all trees, with two unambiguous synapomorphies, character-3 (state = 2) and character-4 (state = 2), representing the *alpha* pattern. The *Buthus* group node is supported by two-thirds of the trees with an ambiguously distributed character-2 (state = 1, d_3 internal to DM_c), a potential synapomorphy. Note that six genera in this group form a clade based on the absence of the tibial spur (character-6, state = 2); however, we consider this clade to be artificial and therefore it most probably does not represent a monophyletic group. The clade (*Ananteris* group + (*Isometrus* group + (*Charmus* group + (*Uroplectes* group + *Tityus* group)))) is supported by two-thirds of the trees and represents an interesting ladderization of these groups. This clade is distinguished from the *Buthus* group by character-2 (state = 0, d_3 external to DM_c), which forms a potential synapomorphy. This clade includes both *beta* and *alpha* scorpions. The outside clade, the *Ananteris* group, represents a “pure” form of the *beta* scorpions, with femoral trichobothrium d_2 located on the dorsal surface. The next clade in this ladderization, the *Isometrus* group, represents a modified *beta* pattern, closer to the *alpha* pattern with d_2 located either on the dorso-internal carina or the internal surface. Continuing, the next clade, (*Charmus* group + (*Uroplectes* group + *Tityus* group)), represents *alpha* scorpions, with d_2 posi-

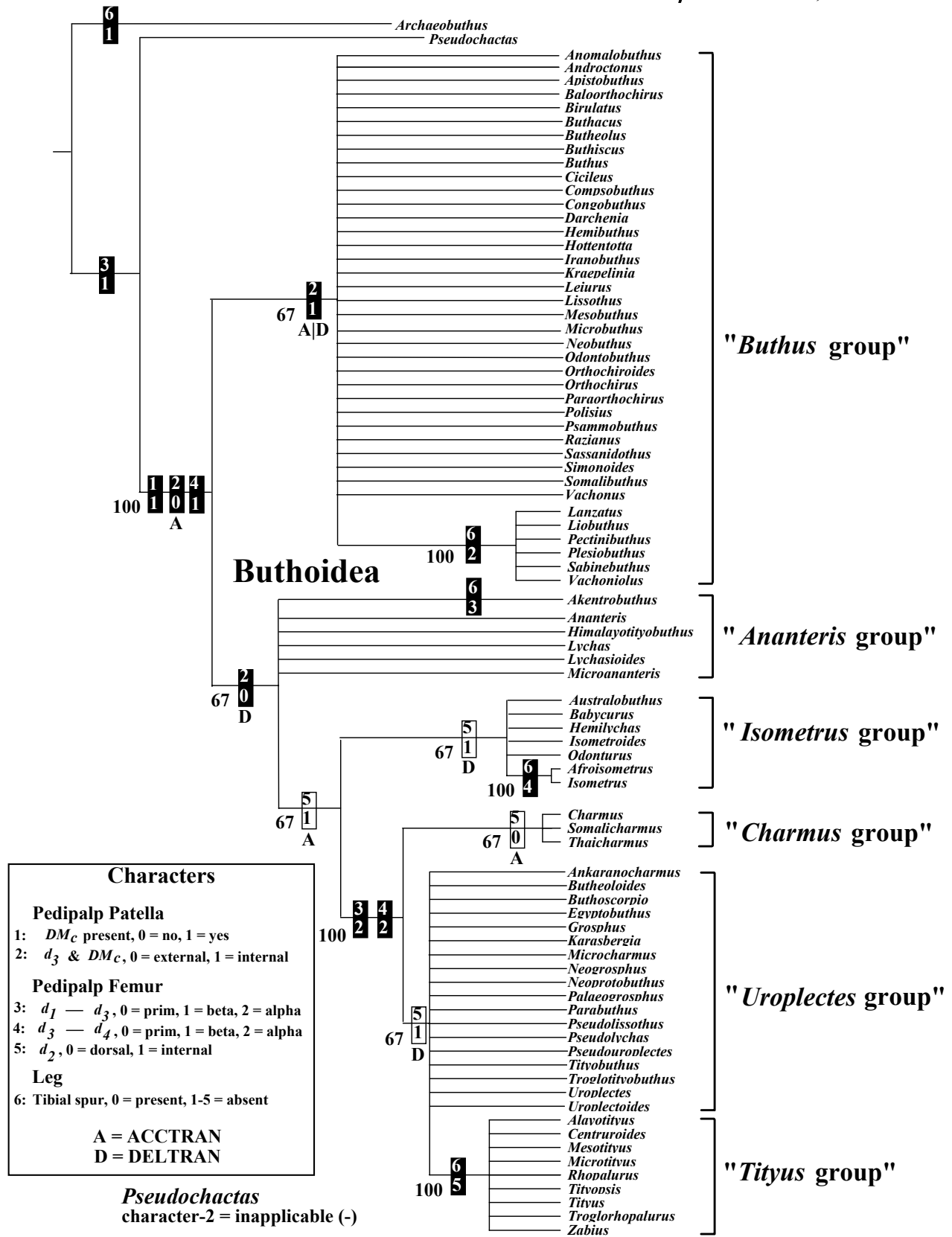


Figure 23: Cladogram showing majority-rule consensus of 9 MPTs for upper-level phylogeny of superfamily Buthoidea with characters distributed. Assumes character-2 (trichobothrium d_3 position with respect to DM_c carina) as inapplicable (-) for *Pseudochactas*. Six partially defined clades are identified by the name of the group of genera. Characters 3 and 4 are ordered. Ambiguous character distribution is identified with the A(CCTRAN) and/or D(ELTRAN) designation. Consensus tree support (a percentage) is presented under each branch. Tree support: length/CI/RI/G-Fit = 14/0.9286/0.9931/-5.750. Open rectangles depict homoplasious characters. Character number depicted on top and character state on bottom.

tion variable. In the *Charmus* group, d_2 is located on the dorsal surface, a *beta* characteristic. Finally, for the clade (*Uroplectes* group + *Tityus* group), we see the pure form of the *alpha* pattern, d_2 located on the internal surface of the femur. What is particularly inviting about the ladderization of the clade identified by d_3 external to DM_c , is the gradual change from a pure *beta* form, as seen in the *Ananteris* group, to the pure *alpha*, as exhibited in the clade (*Uroplectes* group + *Tityus* group), with the *Isometrus* and *Charmus* groups forming intermediate stages. Of course, it must be stressed here that this topology is based only on six characters.

Figure 24 depicts the topology when character-2 is assigned an unknown (?) state to *Pseudochactas*. Except for the minor distributional changes for character-2 (state = 0), the result is identical to the previous topology discussed in detail, including consensus support and overall tree support data.

Figure 25 presents two cladograms where we specifically assigned a state value to *Pseudochactas* for character-2: trichobothrium d_3 located *external* to the (nonexistent) DM_c carina and, trichobothrium located *internal* to the carina. Predictively, for the case where we assume d_3 external to DM_c as primitive to the buthoids, we see d_3 internal to DM_c as an unambiguous synapomorphy for the *Buthus* group and the clade (*Ananteris* group + (*Isometrus* group + (*Charmus* group + (*Uroplectes* group + *Tityus* group)))) is not supported. In contrast, if we assume d_3 internal to DM_c , then the *Buthus* group is undefined and the clade (*Ananteris* group + (*Isometrus* group + (*Charmus* group + (*Uroplectes* group + *Tityus* group)))) is defined unambiguously. Of course, all other clades discussed above under different assumptions (Figs. 23 and 24) remain the same.

The overall support data is quite high for this minimal character set, with only one character, character-5, exhibiting homoplasy, resulting in length/Consistency Index (CI)/Retention Index (RI)/Goloboff-Fit (G-Fit) = 14/0.9286/0.9932/-5.750 (see Kitching et al., 1998, for definition of terms). Table 2 shows the majority-rule consensus for all four cladistic sequences where we see consistency across these sequences in those clades where 100 % MPTs are found, or where no support is exhibited. Predictively, the two clades that are delineated by the location of d_3 with respect to DM_c (character-2) are contrasted with either 100 % support or no support depending on the assigned polarity via *Pseudochactas*.

Character distribution

We present the distribution of character derivations of the four cladistic sequences discussed above for all clades resulting in these analyses (see cladograms in Figs. 23–25, identified in this section as 1, 2, 3, and 4, respectively, for location of these nodes). Each derivation (a potential synapomorphy) is described as follows:

character_number (*old_state* = *value1* → *new_state* = *value2*, *U(nambiguous)* | *A(CCTRAN only)* | *D(ELTRAN only)*, *valid_sequences*) followed by a brief verbal description. *Value1* and *value2* = 0 - n|(-) = integer|inapplicable; *valid_sequences* = which cladistic sequences comply (1, 2, 3, and/or 4). Consult the discussion above for a detailed description of referenced characters and their state values.

Archaeobuthus. Character 6 (state=0 → state=1, U, 1–4): tibial spurs absent (lost).

Pseudochactas + Buthida. Character 2 (state=(-) → state=0, A, 2): patellar trichobothrium d_3 external to DM_c ; Character 3 (state=0 → state=1, U, 1–4): femoral trichobothria d_1 – d_3 angles towards DE_c .

Buthida. Character 1 (state=0 → state=1, U, 1–4): patellar DM_c carina present; Character 2 (state=(-) → state=0, A, 1): patellar trichobothrium d_3 external to DM_c ; Character 4 (state=0 → state=1, U, 1–4): femoral trichobothria d_3 – d_4 angles towards DI_c .

Buthus group. Character 2 (state=(-)|0 → state=1, A|U, 1,2|3): patellar trichobothrium d_3 internal to DM_c .

Lanzatus + Liobuthus + Pectinibuthus + Plesiobuthus + Sabinebuthus + Vachoniolus. Character 6 (state=0 → state=2, U, 1–4): tibial spurs absent (lost). [Note that this clade is considered artificial]

Ananteris + Isometrus + Charmus + Uroplectes + Tityus groups. Character 2 (state=(-)|0 → state=0, D|U, 1,2|4): patellar trichobothrium d_3 external to DM_c .

Ananteris group. No character support, all sequences.

Akentrobuthus. Character 6 (state=0 → state=3, U, 1–4): tibial spurs absent (lost).

Isometrus + Charmus + Uroplectes + Tityus groups. Character 5 (state=0 → state=1, A, 1–4): femoral trichobothrium d_2 located on DI_c or internal surface.

Isometrus group. Character 5 (state=0 → state=1, D, 1–4): femoral trichobothrium d_2 located on DI_c or internal surface.

Afroisometrus + Isometrus. Character 6 (state=0 → state=4, U, 1–4): tibial spurs absent (lost).

Charmus + Uroplectes + Tityus groups. Character 3 (state=1 → state=2, U, 1–4): femoral trichobothria d_1 – d_3 angles towards DI_c ; Character 4 (state=1 → state=2, U, 1–4): femoral trichobothria d_3 – d_4 angles towards DE_c .

Charmus group. Character 5 (state=1 → state=0, A, 1–4): femoral trichobothrium d_2 located on dorsal surface.

Uroplectes + Tityus groups. Character 5 (state=0 → state=1, D, 1–4): femoral trichobothrium d_2 located on internal surface.

Uroplectes group. No character support, all sequences.

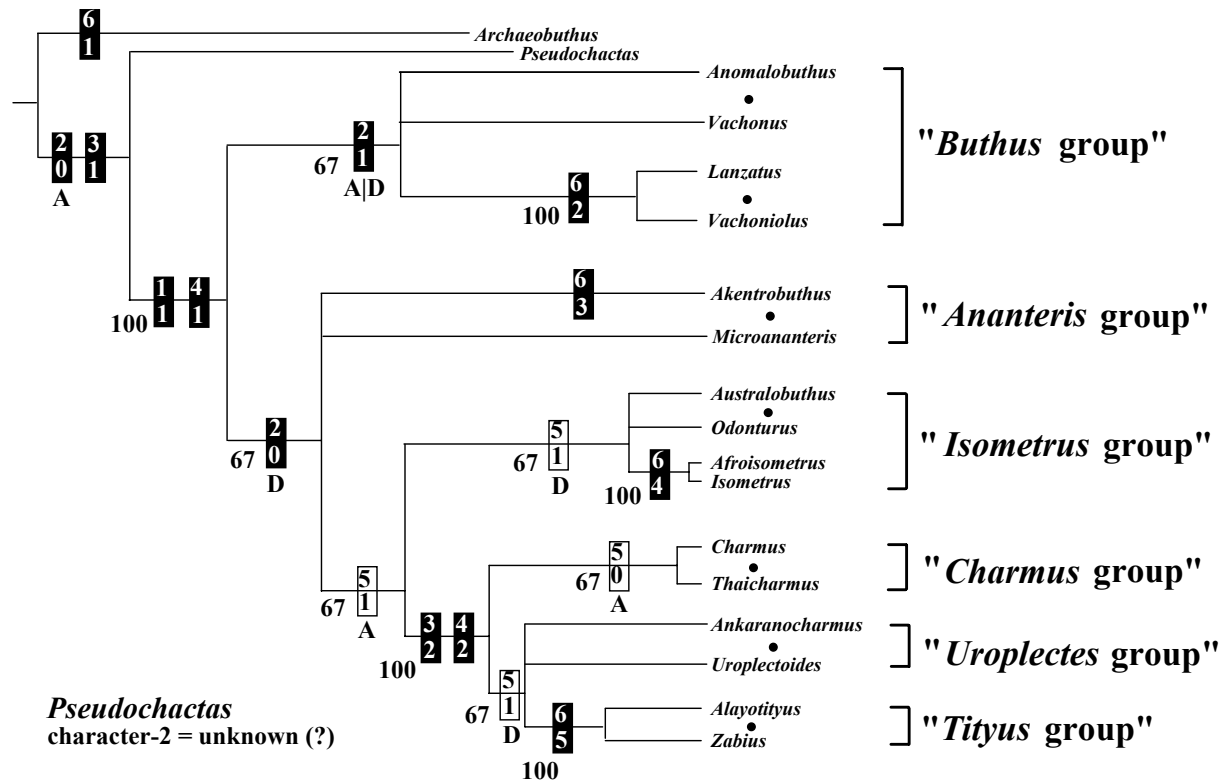


Figure 24: Cladogram showing majority-rule consensus of 9 MPTs for upper-level phylogeny of superfamily Buthoidea with characters distributed. Assumes character-2 (trichobothrium d_3 position with respect to DM_c carina) as unknown (?) for *Pseudochactas*. Six partially defined clades are identified by the name of the *group of genera* (see Fig. 23 for group contents and character definitions). Characters 3 and 4 are ordered. Ambiguous character distribution is identified with the A(CCTRAN) or D(ELTRAN) designation. Consensus tree support (a percentage) is presented under branch. Open rectangles depict homoplasious characters. Character number depicted on top and character state on bottom.

Tityus group. Character 6 (state=0 → state=5, U, 1–4): tibial spurs absent (lost).

Homoplasy

Character-5, the position of femoral trichobothrium d_2 , is the only character that exhibits homoplasy (CI = 0.500). This character is incongruent with characters 3 and 4, the orientation of trichobothria d_1 , d_3 , and d_4 . From a pure cladistic perspective, the homoplasy was reflected in character-2 instead of characters 3 and 4 simply for reasons of parsimony, a smaller number of steps to resolve the incongruency (i.e., if characters 3 and 4 were stipulated as homoplasious, we would have an additional step). Based on the distribution of character-2 (see Figs. 23–25 and distribution discussion above) we see two solutions to this incongruency: (1) for “delayed optimization”, we see the derivation to the internal surface occurring twice, in the *Isometrus* group, a *beta* scorpion group, and in the (*Uroplectes* group + *Tityus* group) clade, both *alpha* scorpion groups; and (2) for “accelerated optimization”, we again see two derivations, migration to the internal surface at the node separating (*Isometrus* group + (*Charmus* group + (*Uroplec-*

tes group + *Tityus* group))), and a reversal in the *Charmus* group, the trichobothrium migrating “back” to the dorsal surface.

Since the location of d_2 in the *Isometrus* group is somewhat equivocal between the dorsointernal carina and the internal surface, whereas, in the clade (*Uroplectes* group + *Tityus* group), we see a more consistent internal surface location, we consider these as separate derivations, which probably should be given separate state values. We believe that this scenario is more plausible than a reversal in the *Charmus* group. Therefore, for any subsequent buthoid analysis, we strongly recommend that these two instances of internal location of trichobothrium d_2 be assigned separate character states (it is also, by the way, a weaker assumption).

Buthoid group definitions

We consolidate the six suggested buthoid groups in this section by providing diagnoses based on the small character set evaluated in this paper. We also sketch out their biogeographical affinities. See Table 1 for a list of genera assigned to these six groups, representing all 82 genera currently assigned to superfamily Buthoidea. In

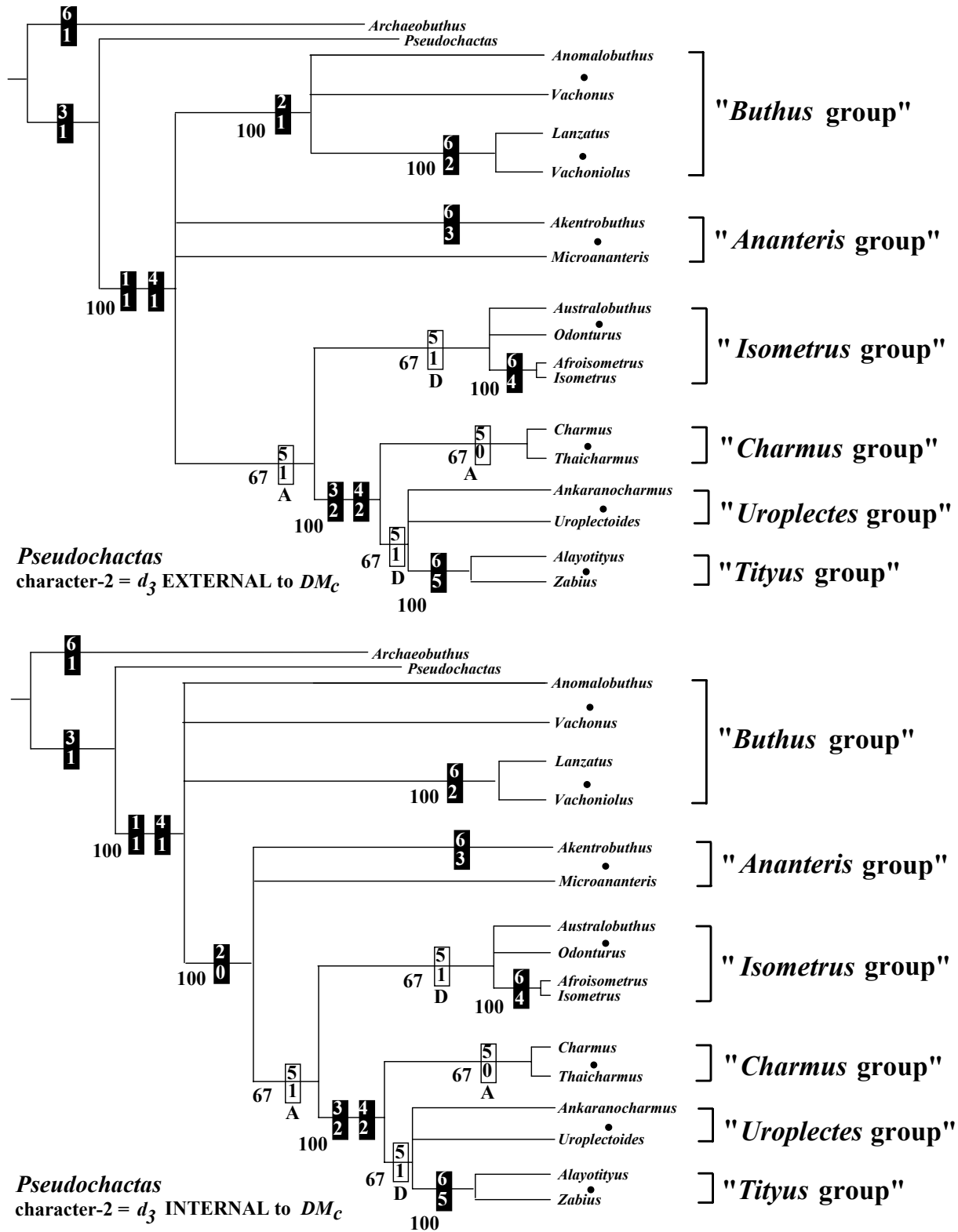


Figure 25: Cladograms showing majority-rule consensus of 3 MPTs for upper-level phylogeny of superfamily Buthoidea with characters distributed. Top cladogram assumes trichobothrium d_3 is located external to (the nonexistent) DM_c carina in *Pseudochactas*; bottom cladogram assume trichobothrium is located internal to DM_c carina. Six partially defined clades are identified by the name of the group of genera (see Fig. 23 for group contents and character definitions). Characters 3 and 4 are ordered. Ambiguous character distribution is identified with the A(CCTRAN) or D(ELTRAN) designation. Consensus tree support (a percentage) is presented under branch. Open rectangles depict homoplasious characters. Character number depicted on top and character state on bottom.

the diagnoses, we list synapomorphies, potential synapomorphies (i.e., ambiguously distributed characters), and symplesiomorphies. Note, in two cases, only symplesiomorphies compose the diagnosis (i.e., the groups are not phylogenetically defined).

Buthus group. Diagnosis: femoral trichobothrium d_2 located on dorsal surface; femoral trichobothria d_1-d_3 angles towards DE_c ; femoral trichobothria d_3-d_4 angles towards DI_c ; patellar trichobothrium d_3 internal to DM_c ; tibial spurs are predominantly present. Geographical distribution: 39 genera: predominantly Palearctic genera, a few species spread to adjacent zones in Afrotropical and Oriental regions; no Neotropical, southern Afrotropical, Madagascar, or Australian forms.

Ananteris group. Diagnosis (no synapomorphies): femoral trichobothrium d_2 located on dorsal surface; femoral trichobothria d_1-d_3 angles towards DE_c ; femoral trichobothria d_3-d_4 angles towards DI_c ; patellar trichobothrium d_3 external to DM_c ; tibial spurs are predominantly present. Geographical distribution: six genera: one Afrotropical-Neotropical (*Ananteris*) and one closely related Neotropical (*Microananteris*); one widely ranging Afrotropical-Oriental-Australian (*Lychas*); two Afrotropical (*Lychasioides*, *Akentrobuthus*); and one Oriental (*Himalayotityobuthus*).

Isometrus group. Diagnosis: femoral trichobothrium d_2 located on internal surface or dorsointernal carina; femoral trichobothria d_1-d_3 angles towards DE_c ; femoral trichobothria d_3-d_4 angles towards DI_c ; patellar trichobothrium d_3 external to DM_c ; tibial spurs are predominantly present. Geographical distribution: seven genera: three Afrotropical (*Afroisometrus*, *Babycurus*, *Odonturus*); three Australian (*Australobuthus*, *Hemilychas*, *Isometroides*); one widely ranging Afrotropical-Oriental-Australian (*Isometrus*). No Neotropical forms.

Charmus group. Diagnosis: femoral trichobothrium d_2 located on dorsal surface; femoral trichobothria d_1-d_3 angles towards DI_c ; femoral trichobothria d_3-d_4 angles towards DE_c ; patellar trichobothrium d_3 external to DM_c ; tibial spurs are predominantly present. Geographical distribution: a closely related group of three genera, Oriental (*Charmus*, *Thaicharmus*) and Afrotropical (*Somalicharmus*). No Neotropical or Australian forms.

Uroplectes group. Diagnosis (no synapomorphies): femoral trichobothrium d_2 located on internal surface; femoral trichobothria d_1-d_3 angles towards DI_c ; femoral trichobothria d_3-d_4 angles towards DE_c ; patellar trichobothrium d_3 external to DM_c ; tibial spurs are predominantly present. Geographical distribution: 18 genera; eight are Afrotropical (*Butheoloides*, *Egyptobuthus*, *Karasbergia*, *Parabuthus*, *Pseudolissothus*, *Pseudolychas*, *Uroplectes*, *Uroplectoides*); nine are Madagascar endemics (*Ankaranocharmus*, *Grosphus*, *Microcharmus*, *Neogrosphus*, *Neoprotobuthus*, *Palaeogrosphus*, *Pseudouroplectes*, *Tityobuthus*, *Troglotityobuthus*); one Ori-

ental (*Buthoscorpio*). No Neotropical or Australian forms. Note that the Madagascar genera also include those currently separated under the family Microcharmidae (*Ankaranocharmus*, *Microcharmus*, *Neoprotobuthus*); however, this placement does not indicate that we endorse here the formal synonymy of Microcharmidae with Buthidae.

Tityus group. Diagnosis: femoral trichobothrium d_2 located on internal surface; femoral trichobothria d_1-d_3 angles towards DI_c ; femoral trichobothria d_3-d_4 angles towards DE_c ; patellar trichobothrium d_3 external to DM_c ; tibial spurs absent. Geographical distribution: 9 genera; all Neotropical.

Historical biogeography

The following observations can be made regarding the historical biogeography of buthoid groups of genera separated in our phylogenetic trees.

The numerous *Buthus* group includes 39 predominantly arid-adapted Palearctic genera, many endemic to southern parts of the Palearctic region (especially North Africa and Middle East). Some of these genera lost tibial spurs, probably several times. The most recent common ancestor of this group probably had a Laurasian origin, and the observed arid-adapted radiation could have been a Tertiary event. However, the lineage itself clearly represents one of the two major, ancient surviving clades with their roots likely in Pangea.

The second clade encompasses 43 genera separated into five groups. These are predominantly Afrotropical genera; very few of them are spread across Afrotropical, Oriental, and Australian regions (*Lychas*, *Isometrus*). It includes also a few Oriental and Australian genus-level endemics, and a separate Neotropical clade of nine genera. The modern Afrotropical region appears to be the major center of diversity for this buthoid clade, and it could be also its center of origin.

The important Oligocene Baltic amber fossils (ca. 60 Mya) exhibit features of at least three genera groups not found currently in the northern fragments of Pangea. Therefore, we can assume that several ancient buthoid groups were present in both Laurasian and Gondwanan parts as late as in the Tertiary, thus surviving the K-T extinction. The evidence for this are the genera *Palaeolychas* (which can be tentatively placed in the *Isometrus* group), *Palaeoakentrobuthus* (which can be tentatively placed in the *Charmus* group), and *Palaeoananteris* (which appears to belong to an extinct buthoid lineage). The extinction of these arboreal (found in amber) groups with the increased Tertiary aridization in the Palearctic region and subsequent Pleistocene glaciations seems a very realistic scenario.

The *Ananteris* group (six *beta* genera) presents an interesting, relict, and probably non-monophyletic assemblage surviving now only in some fragments of

	Inapplicable (-)	Unknown (?)	DM_c / d_3 Primitive	d_3 / DM_c Primitive	Total Support
<i>Buthus</i> group	6 (67 %)	6 (67 %)	3 (100 %)	0	15 (63 %)
<i>Ananteris</i> group	0	0	0	0	0
<i>Isometrus</i> group	6 (67 %)	6 (67 %)	2 (67 %)	2 (67 %)	16 (67 %)
<i>Charmus</i> group	6 (67 %)	6 (67 %)	2 (67 %)	2 (67 %)	16 (67 %)
<i>Uroplectes</i> group	0	0	0	0	0
<i>Tityus</i> group	9 (100 %)	9 (100 %)	3 (100 %)	3 (100 %)	24 (100 %)
<i>A + I + C + U + T</i>	6 (67 %)	6 (67 %)	0	3 (100 %)	15 (63 %)
<i>I + C + U + T</i>	6 (67 %)	6 (67 %)	2 (67 %)	2 (67 %)	16 (67 %)
<i>C + U + T</i>	9 (100 %)	9 (100 %)	3 (100 %)	3 (100 %)	24 (100 %)
<i>U + T</i>	6 (67 %)	6 (67 %)	2 (67 %)	2 (67 %)	16 (67 %)

Table 2: Tree data (majority-rule consensus) supporting the monophyly of the six hypothesized buthoidea groups based on all possible combinations of polarity assignments for the d_3 - DM_c character as assigned to outgroup genus *Pseudochactas*: Inapplicable (-), unknown (?), trichobothrium d_3 is aligned external to the DM_c carina, and d_3 is aligned internal to the DM_c carina. Data specifies number of trees (and their percentage (%) of all trees) supporting monophyly of each clade. Note, there is no support for the *Ananteris* and *Uroplectes* groups, whereas the other groups are supported at least by 63 % of the trees. White on black data areas show the two clades that are affected by the polarity of this character, exhibiting either 0 % or 100 % support, depending on the polarity assignment. *A* = *Ananteris* group, *I* = *Isometrus* group, *C* = *Charmus* group, *U* = *Uroplectes* group, *T* = *Tityus* group.

Gondwanaland, with an especially interesting Afrotropical-Neotropical genus *Ananteris*. The genus *Lychas* is very common and widespread in the Oriental region. Notably, none of the genera in this group evolved any adaptations to arid habitats.

The *Isometrus* group (seven *beta* genera) also appears to include an assemblage of relict origin: four Afrotropical and three Australian genera, and one widely ranging genus of presumable Oriental origin (*Isometrus*). Among these genera, *Afroisometrus* and *Isometrus* lost tibial spurs.

The remaining three groups represent a clade with *alpha* configuration (Vachon, 1975), a clear synapomorphy of 30 buthoid genera, mostly Afrotropical (18) and Neotropical (nine); the group includes four Oriental and no Australian forms. The origin of this clade probably predates the fragmentation of Gondwanaland, judging from the information presented below.

A small *Charmus* group of two Oriental and one Afrotropical genera forms an outgroup to the final clade of (*Uroplectes* group + *Tityus* group). The large *Uroplectes* group (monophyly of which, however, is not confirmed) encompasses 18 genera, all found in the Old World; eight of these genera are Afrotropical; nine are Madagascar endemics, including all three genera of Microcharmidae; and one is Oriental (*Buthoscorpio*). The fact that all endemic Madagascar buthoids are nested within this Afrotropical-Oriental group indicates that most buthoid groups discussed here should have evolved long before the separation of Madagascar (and India) from the African plate. Separation of the block including Madagascar and India from Africa is dated 165–121 Mya (late Jurassic-early Cretaceous) (Vences et al., 2001; Chakrabarty, 2004). Fig. 26 shows the position of continental plates in Early Jurassic (195 Mya), just

before the fragmentation of Gondwanaland started. Judging from their geographical distribution, by this time all six groups of buthoid scorpions outlined in our phylogeny should have been already present in various fragments of Laurasia and Gondwanaland (compare with the discussion on historical biogeography of Hemiscorpiidae by Soleglad et al., 2005). The common ancestor of the genera belonging to the *Uroplectes* group, therefore, should have been present at least in the African portion of Gondwanaland prior to the Jurassic.

A clear synapomorphy of tibial spur loss separates nine genera in a Neotropical *Tityus* group. There can be no doubt that this group (i.e. all New World buthoid genera except *Ananteris* and *Microananteris*) is a derived lineage of buthoids. It should have been separated from its Afrotropical relatives (*Uroplectes* group) with the Western Gondwanaland fragmentation and formation of South America. By most recent estimates, the split of South America from Africa is dated 101–86 Mya (mid-Cretaceous) (Vences et al., 2001; Chakrabarty, 2004). The representatives of *Tityus* group could have reached North America already by the Tertiary and long before the Panama Isthmus formation, probably via the Caribbean stepping-stones (as evidenced by the Eocene *Uintascorpio*; Santiago-Blay et al., 2004b), and had ample time for producing an independent arid-adapted forms represented by the sole North American genus *Centruroides* (known from the Miocene). However, since the deserts of the New World are much younger, and also probably since most arid niches in North America were occupied by Vaejovidae and Caraboctonidae, and in South America, by Bothriuridae and Caraboctonidae, the Buthoidea in the New World never exhibited such radiation in the deserts as in the Old World.

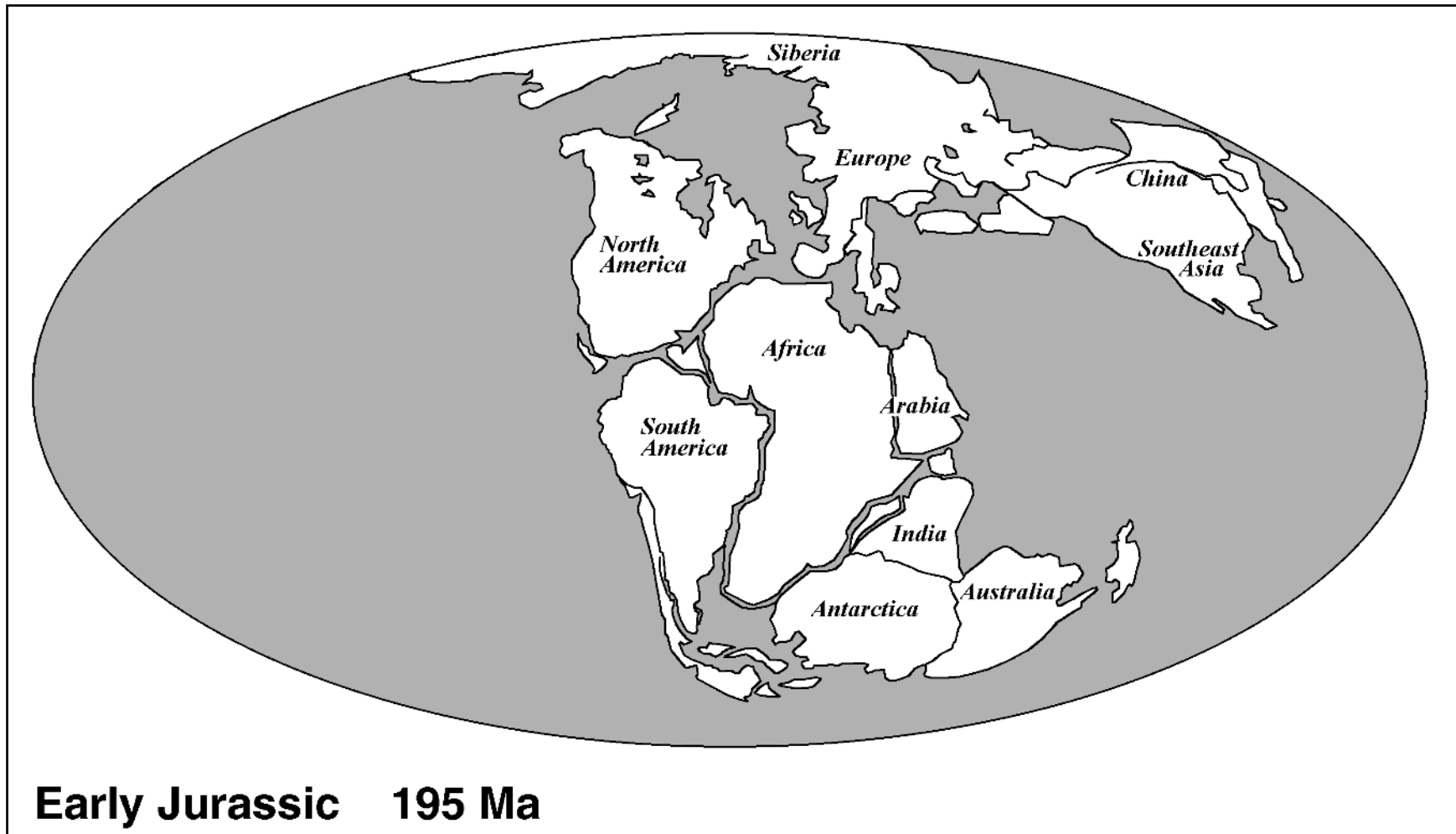


Figure 26: Position of continental plates in early Jurassic period (195 Mya) (after Scotese, 2001, in part).

Further discussion

Fet et al. (2003) presented the first pilot DNA phylogeny including 17 genera of Buthidae based on a small fragment of mitochondrial 16S rRNA gene. Of these, a well-supported monophyletic clade of 13 Palearctic *beta* genera falls completely within our *Buthus* group. On the other hand, four remaining genera (*Lychas*, *Grosphus*, *Centruroides*, and *Rhopalurus*) formed a topology following that presented in this paper, with the Old World *Lychas* (*Ananteris* group) forming an outgroup to three remaining *alpha* genera. The well-supported monophyletic clade of *Grosphus* (*Uroplectes* group) and *Centruroides* + *Rhopalurus* (*Tityus* group), revealed by this pilot DNA phylogeny, is in full agreement with the morphology-based phylogeny presented in our current paper. Further DNA sequence analysis of additional *Tityus* group genera (*Alayotityus*, *Microtityus*, *Tityus*; R. Teruel & V. Fet, in progress) confirms their grouping with the Madagascan *alpha* genus *Grosphus* (*Uroplectes* group). These preliminary molecular data should be supplemented with much more DNA information in order to resolve deep monophyletic lineages.

A very interesting, if also partial, corroboration of buthoid relationships keeps coming from the data provided by toxicology research. For a long time it was known that "Old World" and "New World" Buthidae have pharmacologically different toxins. In fact, this knowledge derives almost exclusively from two groups of buthoids limited to a few highly toxic genera: in the Old World, these are *Androctonus*, *Buthus*, *Hottentotta*, *Leiurus*, *Mesobuthus*, and *Orthochirus*; and in the New World, *Centruroides* and *Tityus*. These two groups, in our phylogenetic scheme, appear at the extremes of buthoid phylogeny: the first one represents the d_3/DM_c *beta* genera (*Buthus* group) while *Centruroides* and *Tityus* belong to the *Tityus* group, i.e. the New World branch of DM_c/d_3 *alpha* group (with their synapomorphic tibial spur loss).

Froy & Gurewitz (2003) published a phylogenetic tree for several classes of buthoid sodium channel toxins (alpha- and beta-toxins). They considered beta-like toxins ancestral, and suggested that in the Old World, they gave rise to mostly excitatory and depressant toxins; and in the New World, to a new, independent type of toxin group (alpha-prime toxins). An ancestral beta-toxin was also recently discovered in *Leiurus* (Gordon et al., 2003).

We can interpret the toxin information in the following way:

(a) excitatory and depressant toxins are clearly a synapomorphy of the Laurasian, arid-adapted *Buthus* group, including mammal-specific toxins, which probably evolved under Tertiary aridization and increased predation pressure from small mammals (Fet et al., 2003);

(b) modern beta-toxins are a synapomorphy of the New World *Tityus* group;

(c) so-called alpha-prime toxins, found only in *Centruroides*, are most likely a synapomorphy of this genus, which also belongs to the *Tityus* group.

It is important to note that, in the phylogeny of Froy & Gurewitz (2003), a so-called birtoxin, known from the Afrotropical genus *Parabuthus*, clusters with the *Tityus* group toxins. This would be expected from our independent morphology-based phylogeny since *Parabuthus* belongs to the *Uroplectes* group. The further toxin knowledge for the *Uroplectes* group as well as other groups of genera (first of all from the *Ananteris* and *Iso-metrus* groups) could prove important in further understanding of buthoid phylogeny as well as the evolution of their toxins.

At this moment, we refrain from any nomenclatural endorsements in assigning taxonomic names to the groups of buthoid genera distinguished in this analysis. As demonstrated by Fet & Lowe (2000), most names historically offered for the subfamilies of Buthidae have never been formally synonymized and technically remain not only available but also valid. These names should be applied as soon as monophylies in Buthoidea are clarified. Further ongoing research (Fet et al., in progress) addressing a multiple character set will possibly lead to a better understanding of phylogeny and systematics of Buthoidea.

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