A NEW SPECIES OF SCORPION IN THE "CHARMUS" GROUP FROM INDIA (SCORPIONES: BUTHOIDEA)

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Abstract: A new species, Thaicharmus lowei sp. n., is described from India. This is the second described species of Thaicharmus, a genus previously known only from Thailand. The genus, a member of the "Charmus" group of the superfamily Buthoidea, is compared to other genera in its group. The taxonomic placement of the "Charmus" group is discussed in connection with the overall phylogeny of the superfamily Buthoidea.

Key words: Scorpiones, Buthoidea, Thaicharmus lowei sp. n., India.

Una nueva especie de escorpión del grupo "Charmus", de la India, (Scorpiones: Buthoidea)

Resumen: Se describe una nueva especie de escorpión de la India, Thaicharmus lowei sp. n. Esta es la segunda especie descrita del género Thaicharmus, conocido previamente tan solo de Tailandia. Se compara el género, perteneciente al grupo "Charmus" de la superfamilia Buthoidea, con otros géneros del grupo. Se discute la posición taxonómica del grupo "Charmus" y sus relaciones filogenéticas dentro de la superfamilia Buthoidea.

Palabras clave: Scorpiones, Buthoidea, Thaicharmus lowei sp. n., India.

Taxonomy/Taxonomía: Thaicharmus lowei sp. n.

Introduction

A new species of the genus Thaicharmus Kovařík, 1995 is described and compared to the only other species in this genus, T. mahunkai Kovařík, 1995. Thaicharmus, a member of the "Charmus" group of superfamily Buthoidea (Fet et al., 2005), is compared to the other two genera assigned to this group, Charmus Karsch, 1879 and Somalicharmus Kovařík, 1998. New characters defining this group are described and the taxonomic placement of this group within superfamily Buthoidea is discussed, based on the original analysis presented in Fet et al. (2005). Biogeographical considerations are presented, further supporting the "Charmus" group.

The subject of sternum "shape" is revisited as it applies to Thaicharmus and related genera, showing again, as demonstrated in Soleglad & Fet (2003a), that depicting the sternum by "shape" is completely bogus leading to entirely superficial taxonomic relationships.

Methods and Material

Terminology and conventions

The systematics adhered to in this paper is current and therefore follows the classification as established in Fet & Soleglad (2005) and buthoid group affiliation follows that suggested in Fet et al. (2005). Trichobothria terminology follows that established in Vachon (1974, 1975). Terminology describing pedipalp chelal carination and finger dentition follows that described and illustrated in Soleglad & Sissom (2001). The sternum terminology follows that in Soleglad & Fet (2003a). The metasomal and pedipalp carination, and leg tarsus armature terminology follows that described and illustrated in Soleglad & Fet (2003b).

Cladistic analysis software packages

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

Systematics

Order SCORPIONES C. L. Koch, 1850

Suborder Neoscorpiones Thorell et Lindström, 1885 Infraorder Orthosterni Pocock, 1911 Parvorder Buthida Soleglad et Fet, 2003 Superfamily Buthoidea C.L. Koch, 1837

Family Buthidae C.L. Koch, 1837

Thaicharmus lowei sp. nov.

Figs. 1–14; Table I.

HOLOTYPE. Female, Sanguem, Goa, India; semidry monsoon forest, under a rock, Feb 2005 (V. Fura & B. Velas). Deposited in the private collection of František Kovařík (Prague, Czech Republic).

MALE unknown.

DIAGNOSIS. Small scorpion with distinct dark variegated patterns on carapace, mesosoma, pedipalpal femur and patella, and trochanter, femur and patella of legs; metasoma with pale variegated patterns dorsally and ventrally on posterior aspect. Three lateral eyes; metasomal segment V lacking broad posterior process that partially overlaps telson; chelal movable finger with 11 denticle groups (inclu-

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Fig. 1. Thaicharmus lowei, sp. nov., female holotype (top) and collection locality, Sanguem, Goa, India (bottom). Photos by V. Fura.

ding basal group); chelal trichobothria *eb* and *esb* positioned at finger base. Pedipalp chelae not particularly slender, movable finger only 1.5 times as long as palm.

DISTRIBUTION. Known only from type locality.

ETYMOLOGY. Named after our colleague and friend Graeme Lowe, who has contributed to our knowledge of scorpions in many areas, in particular the systematics of family Buthidae.

DESCRIPTION based on holotype female, Figure 1.

FEMALE.

Measurements of holotype are presented in Table I. **Coloration** (Figs. 1, 2, 5, 7, 11–13). Carapace and mesosoma medium brown, with dark brown variegated patterns. Pedipalpal femur and patella light brown with medium to dark brown variegated patterns; chelae pale brown to yellow, lacking patterns. Cheliceral palm light brown with medium brown variegated patterns. Sternites light brown, essentially lacking patterns. Metasomal segment I pale brown with medium brown variegated pattern dorsally, other segments with subtle patterns or lacking altogether dorsally; dusky patterns occur on posterior aspects of segments II–V, extending ventromedially (Fig. 7). Telson light yellow-orange, lacking patterns, with subaculear tubercle and aculeus brown. Leg trochanters, femurs and patellae with medium brown variegated patterns.

Carapace (Fig. 2). Anterior edge exhibiting very broad

Table I: Measurements	(in <i>mm</i>) of	Thaicharmus	<i>lowei</i> sp.	nov.
Female holotype from Sa	inguem, Go	a, India.		

Chausataus	
Characters	¥ Holotype
Total Length	15.80
Carapace Length	1.75
Mesosoma Length	5.60
Metasoma Length	6.45
Metasomal Segment I	
Length/Width	0.95/1.15
Metasomal Segment II	
Length/Width	1.10/1.05
Metasomal Segment III	
Length/Width	1.20/1.05
Metasomal Segment IV	
Length/Width	1.40/1.05
Metasomal Segment V	
Length/Width	1.80/1.05
Telson Length	2.00
Vesicle Length/Width/Depth	1.35/0.90/0.85
Pedipalp length	5.65
Femur Length/Width	1.30/0.55
Patella Length/Width	1.70/0.70
Chela Length	2.65
Palm Length/Width/Depth	1.10/0.65/0.65
Movable Finger Length	1.65
Leg II Coxa Length	0.80
Leg III Coxa Length	1.07
Leg IV Coxa Length	1.52
Sternum Length	0.55
Anterior/Posterior Width	0.40/0.55
Apex Lateral Side Length	0.28
Pectinal Basal Plate Length/Width	0.50/0.50
Pectinal Teeth	15/14

subtle indentation with a conspicuous epistome present medially. Surface somewhat lustrous with scattered minute granules occurring primarily on the variegated patterns. Lateral eyes, in straight line, numbering three, basal eye slightly larger than others. Median eye tubercle and eyes somewhat large, situated well anterior of middle with the following length and width formulas: 55|175 (anterior edge to medium tubercle middle|carapace length) and 38|142 (width of median tubercle including eyes|width of carapace at that point).

Mesosoma (Figs. 5 and 9). Tergites I–VII lustrous, essentially lacking granulation; tergite VII (Fig. 5) with two pairs of carinae, granulate on posterior half. Sternites smooth and lustrous, sternite V lacking carinae. Stigmata (Fig. 9) are short and oval-like.

Metasoma (Fig. 7). Segments I–IV: dorsal carinae granulate on posterior half; dorsolateral carinae granulate on posterior third of segment I, posterior quarter of segments II–IV, with terminus on IV somewhat flared; lateral, ventrolateral and ventromedian carinae essentially obsolete. Segment V: dorsolateral carinae rounded and granulate; lateral, ventrolateral and ventromedian carinae essentially obsolete. Posteroventral aspect of all segments somewhat punctated and granulated in areas where variegated patterns occur, the most exaggerated on metasomal segment V (Fig. 7). Segments I–IV covered with minute short setae.

Telson (Fig. 13). Vesicle somewhat bulbous with a short and highly curved aculeus, the vesicle/aculeus juncture quite distinct. A short, non-granulated, but distinct subaculear tooth present on posterior aspect of vesicle. Vesicle surface covered ventrally and laterally with somewhat large granules and numerous minute setae.

Pectines (Fig. 6). Well developed sclerites, length|width

formula 330|150 (length taken at anterior lamellae|width at widest point including teeth). Sclerite arrangement somewhat complex with three anterior lamellae and irregular shaped middle lamellae, the largest located basally; fulcra present. Minute short setae extend from edge of anterior lamellae. Teeth, numbering 15/14, short basally, lengthening distally and then terminating with a shorter ovoid-shaped tooth. Basal piece composed of a single sclerite, large and square, almost as long as sternum, with wide deep V-shaped indentation along anterior edge.

Genital Operculum. Sclerites oval in shape vertically, showing slight separation at both anterior and posterior junctures.

Sternum (Fig. 8). Type 1, exhibiting minimal horizontal compression; concave region slightly larger than the posterior depression; outer ridge wide and only occurring on posterior edge; conspicuous apical "button" present. Sternum posteriorly as wide as long, apex lateral edge relatively long, approximately one half the sternum length.

Chelicerae. Movable finger dorsal edge with one large subdistal (*sd*) denticle; subbasal (*sb*) denticles quite small and close together; ventral edge with two ventral accessory (*va*) denticles. Ventral distal denticle (*vd*) approximately same length as dorsal (*dd*) counterpart. Ventral surface of fixed finger base with two pigmented *va* denticles.

Pedipalps (Figs. 3, 10–12). Somewhat small appendages, chelal movable finger shorter than carapace and metasomal segment V, and 1.5 times as long as palm; conspicuous pale non-pigmented chela is in strong contrast to femur and patella with dark variegated patterns. Femur (Fig. 11): Dorsointernal carina granulated, ventrointernal carinae serrate, other carina essentially obsolete. Surfaces smooth except for internal, which exhibits six scattered serrated granules. Patella (Fig. 12): All carinae are smooth to obsolete except for well developed Dorsal Patellar Spur (DPSc) carina, exhibiting six serrated granules, and the Ventral Patellar Spur (VPS_c) carina with five serrated granules. All surfaces smooth. Chelal carinae: All carinae are essentially weak to obsolete except for the dorsomarginal (D4) carina which is rounded with scattered granulation. Chelal finger dentition (Fig. 3): median denticle (MD) row groups aligned obliquely and imbricated, numbering eleven for both fixed and movable fingers, including apical and basal groups. Both fingers with eleven inner (ID) denticles. Trichobothrial patterns (Figs. 10-12): Type A, orthobothriotaxic, femur with *alpha* pattern with trichobothrium d_2 located on dorsal surface (i.e., characteristic of "Charmus" group). Femur: trichobothrium e_1 proximal to d_5 . Patella: d_3 trichobothrium positioned on ventral half of segment, presumably external to obsolete DM_c carina; external trichobothrium em aligned horizontally between est and et in a straight line angling distally towards ventral edge. Chela: trichobothria eb and est positioned basally on fixed finger; trichobothria $Eb_1 - Eb_2 - Eb_3$ juncture angles distally forming an inverted V-shape.

Legs (Fig. 4). Both pedal spurs present, tibial spur present on legs III–IV. Tarsus with scattered setae on ventral surface. Coxae not elongated, exhibiting length ratios of 80|107|152 for legs II, III and IV, respectively.

COMPARISON TO OTHER SPECIES IN GENUS. Besides being members of the "Charmus" group in Buthoidea (see discussion below), *Thaicharmus lowei* and *T. mahunkai* Kovařík,



Fig. 2-9. *Thaicharmus lowei* Kovařík, Soleglad & Fet, **sp. nov.**, holotype. **2.** Carapace, showing epistome. **3.** Chelal movable finger showing dentition. **4.** Leg IV showing pedal spurs and tibial spur. **5.** Tergite VII showing carinae. **6.** Right pecten. **7.** Metasomal segment V, ventral view. **8.** Sternum, showing reduced posterior depression and apical "button". **9.** Sternite III (partial) showing right stigma.

1995, share the following important characters: Both species exhibit an epistome on the carapace anterior edge and both have a somewhat robust globular telson equipped with a small but distinct subaculear tubercle. Their pedipalp patellar trichobothria *est*, *em*, and *et* are aligned in a straight line angled distally towards the ventral edge; femoral trichobothrium e_I is positioned proximal to d_5 . Their sternum is roughly as wide as long exhibiting minor horizontal compression (Sternum_L/Sternum_{PW}: *T. lowei* = 1.000, *T. mahunkai* = 1.029); and leg coxae III–IV are short, not elongated as typically exhibited in the Buthoidea (Coxa $III_L/Coxa II_L$ and $Coxa IV_L/Coxa II_L$: *T. lowei* = 1.338 and 1.900, *T. mahunkai* = 1.308 and 2.000). See Soleglad & Fet (2003a: table 2) for a comparison with 30 other buthoid genera. The pectines are constructed similarly with enlarged basal middle lamellae, and both exhibit fulcra.

T. lowei is a smaller species than *T. mahunkai* (16 mm in length for the former species, 29 mm for the latter) with more distinct variegated patterns and less punctations on the metasomal surface. *T. lowei* is equipped with three lateral eyes whereas *T. mahunkai* exhibits four; *T. lowei* lacks the distally expanded metasomal segment V found in *T. ma*-



Fig. 10-13. *Thaicharmus lowei* Kovařík, Soleglad & Fet, **sp. nov.**, holotype. **10-12.** Pedipalp trichobothrial pattern. **10.** Chela, external and ventral views; closed circle on chelal fixed finger external view designates internal trichobothrium *i*. **11.** Femur, dorsal view; circled area shows internal trichobothria of femur from an internal perspective. **12.** Patella, dorsal and external views. **13.** Telson, lateral and ventral views, showing subaculear tooth.

hunkai; and the pedipalp chela in *T. lowei* are not as elongate as in *T. mahunkai*, the movable finger only 1.5 times longer than the palm, whereas in *T. mahunkai*, it is over 2 times longer. Presumably due to the shorter fingers in *T. lowei*, trichobothria *eb* and *est* are positioned near the finger base, not midfinger as seen in *T. mahunkai*.

Due to the structural differences such as the number of lateral eyes, the structure of metasomal segment V, and the elongated chelal fingers with different locations for trichobothria *eb* and *esb*, as well as their somewhat disjoint geographical locations, the two species of *Thaicharmus* may represent two distinct genera. But, since each is only represented by a single species, it is best to wait until additional material is collected from both India and Thailand. If further species are isolated that preserve the differences stated above, then at that time the breakup into two genera would be prudent.

Discussion: the "Charmus" Group of Buthoidea

The "Charmus" group of Buthidae was suggested by Fet *et al.* (2005) based on the analysis of a small but important set of characters, primarily composed of pedipalp femur and patellar trichobothria. Members of this group can be defined as follows: patellar trichobothrum d_3 is positioned external to the dorsomedian (DM_c) carina; femoral trichobothria d_1 , d_3 , and d_4 comply with the *alpha* pattern (Vachon, 1975), and d_2 is located on the *dorsal* surface of the segment. To complete this definition, in the context of Fet *et al.* (2005), members of the "Charmus" group also exhibit tibial spurs on legs III–IV.

Genera distinction

Presently three genera comprise the "Charmus" group: *Charmus* and *Thaicharmus* from Asia, and *Somalicharmus* from Africa (see map in Figure 14). [Note: The type locality of *Somalicharmus whitmanae* Kovařík, 1998 (El Meti) has



Fig. 14. Distribution of "Charmus" group of superfamily Buthoidea. General distribution of genus *Charmus* based on Lourenço (2002: fig. 15, in part). Countries Ethiopia, India, Sri Lanka and Thailand are shaded.

been confirmed to be in Ethiopia (Kovařík & Whitman, 2005: 112) rather than Somalia (Kovařík, 1998). This specimen was collected by the Missione Biologica Sagan-Omo led by Edoardo Zavattari, which in 1939 explored the Borana region from Dolo westwards to Lake Stephanie and the Omo River (Largen, 2001). According to Largen (2001), El Meti is located at 04°58'N 37°08'E, at an altitude of 1500 m.]

All three genera comply to the characters stated above, as well as with other characters listed here. We will first list additional characters shared by these three genera, and will then contrast them with their specific differences. These three genera share a somewhat wide sternum which exhibits minimal horizontal compression, the posterior depression and concave region are minimal and a distinct apical "button" is present (see Fig. 7 for an example of this sternum; also see Kovařik, 1995: fig. 13; Tikader & Bastawade, 1983: figs. 387, 405; Sreenivasa-Reddy, 1966: fig. 10). Lourenco (2002: fig. 4) reports in his description of Charmus minor "... Sternum pentagonal, but strongly flattened; three times wider than long ..." Clearly this species has a very wide sternum but in Lourenco's fig. 4, leg coxa II hangs over the sternum apex and the genital operculum covers a portion of the posterior edge (note, the outer ridge is not visible), so this sternum is definitely a little longer than depicted, but still quite wide. The sterna in Thaicharmus and Somalicharmus are approximately as wide as long, Sternum_L/Sternum_{PW} = 0.933-1.029. These genera exhibit some of the least horizontal compression attributes for leg coxae as discussed in Soleglad & Fet (2003a: table 2), where Thaicharmus and Somalicharmus (leg coxae data for *Charmus* is not available) comprise the shortest leg coxae III and IV of the 32 buthoid genera so far studied: Coxa $III_L/Coxa\ II_L$ = 1.231–1.330 and Coxa $IV_L/Coxa\ II_L$ = 1.900–2.000. The femoral trichobothrium e_1 is placed somewhat basal in these three genera, proximal to trichobothrium d_5 . Since these three diverse genera occur in distinct disjunct geographic locations (i.e., India and Sri Lanka, Thailand, and Ethiopia; see Fet & Lowe, 2000; Lourenco, 2000, 2002; Kovařík & Whitman, 2005), we consider these sternum and leg coxae attributes as well as the femoral trichobothria locations, as potential synapomorphies for the "Charmus" group of Buthidae (see cladistic discussion below).

The three "Charmus" group genera can be separated by the following characters. Genus Charmus does not have a subaculear tooth on the telson, whereas Thaicharmus and Somalicharmus exhibit a small but distinct subaculear tooth. Patellar trichobothria em, est, and et are aligned in a straight line in genus Thaicharmus (em distal to est) whereas in *Charmus* and *Somalicharmus*, the *est–em–et* juncture angles basally on the segment (in particular, it is quite exaggerated in Somalicharmus, em located almost midsegment, closer to esb₁-esb₂). Somalicharmus can be separated from Charmus and Thaicharmus by several unusual trichobothrial subpatterns and positions: chelal trichobothria Eb1-Eb2-Eb3 juncture angles basally, not distally as in the other two genera; d_1 - d_2 and *eb*-*et* are located on the basal half of the fixed finger, whereas in the other genera, *db*–*dt* and sometimes *eb–et*, are positioned on the distal half of the finger; and chelal trichobothrium *i* is positioned midfinger in Somalicharmus (unusual in buthoids) whereas in the other genera, it is placed on the distal aspect of fixed finger's inner edge.

The "pentagonal" sternum

The genus Charmus has been a controversial taxon ever since Birula (1917: 160-163) considered it a member of family Vaejovidae, based solely on the "shape" of the sternum. Sreenivasa-Reddy (1970) perpetuated this theme of the sternum shape further, in his argument that Charmus was indeed a buthid, by showing that Charmus exhibited other buthoid characters, in contrast to Vaejovidae, therefore implicitly agreeing that Charmus and Vaejovidae exhibited the same sternum structure. He even hypothesized a "stress" force that explained the transformation from a "pentagonal" sternum to a "triangular" sternum, thus attempting to minimize their difference. Interestingly, this same theory was independently discussed in detail in Soleglad & Fet (2003a) in their reevaluation of the sternum in scorpions where they used the term "horizontal compression". Of course, Soleglad & Fet (2003a) considered only Type 1 sterna for this hypothesis, having shown that the sternum in family Vaejovidae (and all other Recent scorpion families in parvorder Iurida, termed a type 2 sternum) has an entirely different structure than that found in the Buthoidea, Pseudochactidae, and Chaerilidae. Namely, it is not pentagonal, but instead is formed as a concaved hexagon (= six sides), the



Fig. 15. Cladogram (after Fet *et al.*, 2005: fig. 25, in part) showing upper-level phylogeny of superfamily Buthoidea with characters distributed. Polarity of character-2 is *external* (= 0) and character-5 is represented with three states, dorsal, internal or on carina, and internal. "Charmus" group is contained in gray rectangle. Character number depicted on top and character state on bottom.

posterior edge bifurcated into two edges. See Soleglad & Fet (2003a: fig. 2) for a detailed description of these two distinct sternum types.

Germane to the genera discussed in this paper is the "sternum shape" used in the key to Buthidae genera presented in Sissom (1990: 93-100). We see that genus Charmus (along with Karasbergia Hewitt, 1913 and Butheoloides Hirst, 1925) is separated from genus Buthoscorpio Werner, 1936 (= Pocockius Francke, 1985 in Sissom, 1990) by its "subpentagonal" sternum in contrast to a "subtriangular" sternum in Buthoscorpio. This is interesting indeed since Vachon (1961) states for Stenochirus (= Buthoscorpio) politus: "... Sternum court, pentagonal (resseinblant a celui d'un Scorpionidae) ..." The sterna are quite similar in these two genera, the sternum in Buthoscorpio is slightly longer than wide thus termed "subtriangular" by some and "subpentagonal" by others. Of course, to be truly "triangular" the two apex lateral sides would have to be absent, a condition not found in any known buthid. To further emphasize this point, as discussed in Soleglad & Fet (2003a), a new vaejovid genus Physoctonus Mello-Leitão, 1934 was named from a single specimen, based on its "pentagonal" sternum. As it turned out, this scorpion was a small buthid species (23 mm in length) of Rhopalurus whose sternum is less compressed due to its small size (Francke, 1977: 128, fig. 13).

Buthoidea "Charmus group": *Phylogenetic Considerations*

The present classification of Buthoidea is unclear (Soleglad & Fet, 2003b; Fet et al., 2005); no subfamilies or tribes of Buthidae are defined, and, in addition, relationship of Microcharmidae and Buthidae is not resolved. Fet et al. (2005) based their definition of six buthoid groups of genera primarily on the position of patellar trichobothrium d_3 with respect to the DM_c carina (external or internal to) and the alpha/beta disposition of the dorsal femoral trichobothria $d_1 - d_5$. They performed a complete cladistic analysis of these six characters (which also included the presence/absence of the leg tibial spur) sequencing through all possible polarities of the d_3/DM_c character, using the relic genus *Pseudochac*tas Gromov, 1998 to test its polarity (see Fet et al. 2005: 19-26, figs. 23-25, for a detailed description of this process). Since the Fet et al. (2005) paper, additional data has become available on the d_3/DM_c character with the recent reanalysis of the fossil scorpion Archaeobuthus estephani Lourenço, 2001 (Baptista et al. 2006: figs. 4, 18, 19). In particular, a *complete* revaluation of trichobothria patterns of Archaeobuthus was conducted and it was established, that, (a) the DM_c carina is absent in this genus, (b) patellar trichobothrium d_3 is positioned extremely external to the segment midpoint. Based on this, and the somewhat external position of d_3 in genus *Pseudochactas*, it was suggested by these authors as well as adopted in this paper, that the primitive state for the d_3/DM_c character is an *external* position. Consequently, from the four topologies based on the polarity of this character as exercised in Fet *et al.* (2005), we now obtain the topology depicted in Figure 15.

As recommended in Fet et al. (2005: 24, fig. 2) in their discussion of homoplasy, we adopt the splitting of the character representing the position of femoral trichobothrium d_2 into three states: (1) dorsal, the primitive state; (2) located either on the internal surface or on the dorsointernal carina, the "Isometrus" group; and (3) is always located on the internal surface, the "Uroplectes" and "Tityus" groups. Therefore, the "Charmus" group in this topology, based on this minimal character set, is undefined (i.e., it has no synapomorphies). However, as discussed above, additional characters are being evaluated for this small buthoid group. It is clear that the group is further defined by their somewhat primitive sternum, lacking significant horizontal compression, and the short non-elongated leg coxae III and IV. We suggest here that these characters, and probably others, will prove to be synapomorphic for this small buthoid group. Of course these characters must be analyzed for the other buthoids as well before this can be established.

The topology represented in Fig. 15 is quite interesting for several reasons. Now that we have hypothesized the primitive state for the d_3/DM_c character, we see that the "Buthus" group of genera is defined with a synapomorphy, d_3 positioned internal to the DM_c carina. The "Isometrus" group is defined with its internal placement of the femoral d_2 trichobothrium, otherwise it is a *beta* group. The "Charmus", "Uroplectes", and "Tityus" groups are defined with the fundamental *alpha* pattern, and the latter two groups by a complete *alpha* pattern (i.e., d_2 located on the internal surface of the femur). And finally, the "Tityus" group is defined by the consistent loss of the tibial spur, considered important for these New World buthoids, more so than its hypothesized independent loss seen in other groups.

The position of the "Charmus" group in the cladogram depicted in Fig. 15 is quite revealing. We see that it represents the *most* primitive form of the *alpha* pattern, with femoral trichobothrium d_2 still located on the dorsal surface as it is in the more primitive *beta* buthoids, and therefore, forms the plesiomorphic sister group to the pure *alpha* buthoids (i.e., the "Uroplectes" and "Tityus" groups).

The three genera of the "Charmus" group, found in India (Charmus), Southeast Asia (Thaicharmus) and Ethiopia (Somalicharmus), present an obvious biogeographic disjunction between Africa and Asia. However, one does not have to assign the age of this disjunction to the original Gondwana fragmentation. According to the new model for the tectonic evolution of the Indian plate by Chatterjee and Scotese (1999), in Late Cretaceous (75-70 Mya), India and Africa became temporarily joined by a landbridge, named Greater Somalia. The plate tectonic model of Chatterjee and Scotese (1999) indicates that biotic interchange via Greater Somalia could have been available until about 60 Mya. This connection allowed immigration of many taxa, including dinosaurs, into India from Africa and Europe, and accounts for some spectacular disjunctions (Hedges, 2003; Bossuyt et al. 2006). It is possible that the common ancestor of Charmus and Thaicharmus entered India from Africa, where related Somalicharmus still dwells. This direction seems more plausible than the reverse, since most other groups of Buthoidea appear to have diverged in continental Africa, with further dispersal and differentiation (Fet *et al.*, 2005). Absence of "Charmus" group from the well-studied Madagascar could confirm this dispersal scenario (rather than reverse), since 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).

According to our phylogenetic reconstruction (Soleglad & Fet, 2003b; Fet et al., 2005; Baptista et al., 2006), Buthida diverged from other orthostern parvorders in the late Paleozoic, and diversified through the Mesozoic; note, however, that we place Cretaceous fossil orthosterns Archaeobuthus and Palaeoburmesebuthus well outside parvorder Buthida (with its sole superfamily Buthoidea) (Baptista et al., 2006). By late Cretaceous, all six groups of buthoid scorpions outlined by Fet et al. (2005) should have been already present in various fragments of Laurasia and Gondwanaland. Fet et al. (2005) indicated, for instance, that the Tertiary Baltic (Laurasian) genus Palaeoakentrobuthus could be tentatively included in "Charmus" group. It is obvious that some of the African lineages of Buthoidea could migrate to India via Greater Somalia before or after the K-T extinction (65 Mya), much earlier than the Indian subcontinent joined Asia (ca. 45 Mya). Since the Greater Somalia connection was severed in the Middle Paleocene (60 Mya), this date could be used as a rough calibration for the minimal age of African/Asian disjunction presented by the genera of the extant "Charmus" group.

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