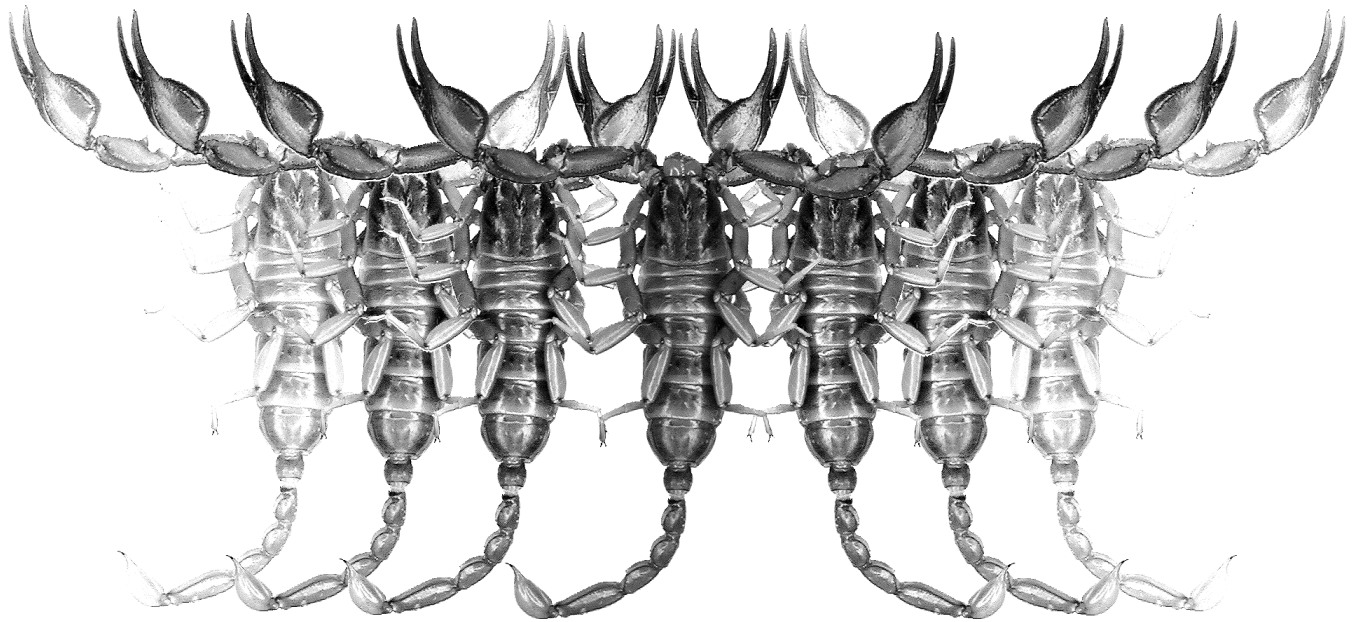# *Euscorpius*

Occasional Publications in Scorpiology

The Scorpion Sternum: Structure and Phylogeny (Scorpiones: Orthosterni)

M.E. Soleglad and V. Fet

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Euscorpius

Occasional Publications in Scorpiology

Euscorpius is the first research publication completely devoted to scorpions (Arachnida: Scorpiones). *Euscorpius* takes advantage of the rapidly evolving medium of quick online publication, at the same time maintaining high research standards for the burgeoning field of scorpion science (scorpiology). *Euscorpius* is an expedient and viable medium for the publication of serious papers in scorpiology, including (but not limited to): systematics, evolution, ecology, biogeography, and general biology of scorpions. Review papers, descriptions of new taxa, faunistic surveys, lists of museum collections, and book reviews are welcome.

Derivatio Nominis

The name *Euscorpius* Thorell, 1876 refers to the most common genus of scorpions in the Mediterranean region and southern Europe (family Euscorpiidae).

Euscorpius is located on Website **'http://www.science.marshall.edu/fet/euscorpius/'** at Marshall University, Huntington, WV 25755-2510, USA.

The scorpion sternum: structure and phylogeny (Scorpiones: Orthosterni)

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"My work is fascinating. To know that the organ, which you are observing, was seen by nobody before; to trace the proportions which nobody *before you thought about; to submerge yourself into a wondrous, crystal world of a microscope, under a royal rule of silence limited by its own horizon; that dazzlingly white arena – all this is so exciting that I have no words".*

Vladimir Nabokov, to his sister, about his studies of Lepidoptera (translated from Russian by V. Fet).

Summary

The structure of the sternum of all major Recent scorpion groups is analyzed in detail. Based on this analysis, two fundamental sternum types are identified, described and illustrated, *type 1* and *type 2*. These sternum types are distinguished by criteria based on external and internal structural features. The sternum types described herein are offered as a replacement for the various characterizations used throughout the last 140 years which emphasize only gross overall shape and proportions. Phylogenetic and taxonomic ramifications of these new sternal types are discussed. The Carboniferous fossil scorpion *Palaeopisthacanthus schucherti* Petrunkevitch is assigned to sternum *type 1*. The *type 1* sternum is also assigned to the three primitive Recent scorpion groups, the pseudochactids, the buthoids, and the chaerilids. Sternum *type 2* is defined for the remaining scorpion groups, those complying with Type C orthobothriotaxy. Based on these assignments, sternum *type 1* is considered primitive. Within these two basic sternal types a hypothesis of horizontal and vertical compression is offered as a cause-effect for the unique sterna of the buthoid and bothriurid scorpions.

Introduction: Sternum Shape in Scorpion Taxonomy

The scorpion sternum is located ventrally between the coxae of legs III and IV. Its origins are equivocal (Dunlop & Webster, 1999): sternum is usually treated as fused sternite plates of somites VII and VIII (Hjelle, 1990); alternatively, it could be a modified pair of opisthosomal appendages, homologous to the metastomal plate of Eurypterida and the chilaria of Xiphosura (Dunlop & Webster, 1999; J. Dunlop, personal communication). Embryological observations (R. Farley, personal communication) appear to be consistent with the sternum (or part of it) originating from the first opisthosomal segment. All fossil scorpions (known from the Silurian) have a sternum. In the systematics of Recent scorpions (order Scorpiones, suborder Neoscorpionina,

infraorder Orthosterni), the sternum shape has been considered an important character at the highest levels (superfamily and/or family). Three geometrical shapes of sterna have been traditionally distinguished: (1) pentagonal, (2) triangular, and (3) transverse.

Peters (1861: 511-512) was the first to assign the scorpion sternum its central position in the order's systematics. He distinguished four family-group taxa of extant scorpions, addressing their sternum shape in the very first sentence of his diagnoses: Telegonini (now Bothriuridae), with a horizontal ("linienformige") sternum; Scorpionini, with sternum "large, square or pentagonal, with parallel lateral sides"; and two groups which now fall under Buthidae: Centrurini and Androctonini, with a "small, triangular" sternum. This basic division of Peters essentially remained the same for the following 140 years, and sternum shape was readily used

by all scorpion systematists who diagnosed or keyed higher taxa.

As many new genera have been described, and diversity of family-group taxa increased, all authorities still concurred on the issue of classifying sternum shapes. Thorell (1876: 6-9) separated all scorpions into four families: family Androctonidae (now Buthidae) as having "narrowing forwards, subtriangular" sternum; Telegonoidae (now Bothriuridae) with a "sternum very short, forming a transverse falciform band or line curved backwards"; and families Vejovoidae and Pandinoidae both having sternum "with parallel sides, subpentagonal". Karsch (1879a: 17-22) listed the same division into three shapes as "transverse", "subtriangular", and "subpentagonal". Pocock (1902: 1) characterized "…sternum with parallel or subparallel sides, pentagonal …" (Vaejovidae) as opposed to "… sternum triangular, with anteriorly converging sides …" (Buthidae). Birula (1917: 15-16) provided a key to all scorpion families recognized at this time, again heavily based on sternum shape. His first key couplet separates Bothriuridae ("sternum consists of two narrow transverse plates; width therefore exceeding several times the length") from other families where "sternum is not more than two times wider than its length, often longer than its width". Next, he separates "pentagonal" (most non-buthids) and "triangular" (most Buthidae) shapes, with a number of additional shape qualifiers. For example, for Buthidae he says "sternum triangular or strongly narrowed anteriorly", and for Euscorpiidae (then under Chactidae), "sternum pentagonal with almost parallel or just slightly convergent lateral sides" (Birula, 1917: 16). He also distinguished, within pentagonal sterna families, "entire" and "tripartite" variants, former for Scorpionidae (now several "scorpionoid" families), latter for Chactidae (which then included also Iuridae and Chaerilidae) (Birula, 1917: 100, 163). In his new proposed classification of the extant scorpions, Birula (1917: 161-164) again classified sternum shapes in three basic categories: pentagonal (entire or tripartite), triangular, and transverse.

Pentagonal versus triangular sternum became a commonplace couplet of any regional or general scorpion family key or monograph, supplemented where appropriate by a reference to transverse shape in Bothriuridae (Hoffmann, 1931: 302; Werner, 1934: 265; Moreno, 1940: 28; Mello-Leitão, 1945: 13; Millot & Vachon, 1949: 396; Williams, 1980: 2, etc.). Stahnke (1957: 78-79, 1970: 302, Fig. 2) described and/or illustrated these sternal types in his papers dealing with scorpion nomenclature. Most recently, Sissom (1990: 72-74) widely used "subtriangular" versus "subpentagonal" shape terminology in his review and key of Buthidae.

It is interesting to see how often the three "basic" shapes are referred to with various forms of qualification, such as equilateral, subpentagonal, subtriangular, triangulo-pentagonal, near-triangular, transverse, slit-

like, much wider than long, etc., and yet many exceptions of taxa placement as associated with these three forms are common. In general, the triangular, subtriangular, near triangular, etc. shapes are associated with the buthoids, but several buthid genera exhibit sterna conforming to the "pentagonal" form as well. The wider than long transverse sterna that are associated with the bothriurids can also be found in some iurids, *Hadrurus* in part, and *Hadruroides* and *Caraboctonus* in particular. The superstitioniid *Superstitionia* also has quite a short, wide sternum.

Kjellesvig-Waering (1986: 15-16) considered all Recent scorpions as having pentagonal sterna (i.e., five sides), noting that the short transverse sternum found in the bothriurids is actually folded vertically and is pentagonal when flattened out (he was quoting Petrunkevitch (1953); this was also quoted in Sissom (1990: 73-74)). From Kjellesvig-Waering's point of reference, it seems that he restricted the "pentagonal" shape to the regular-sided or equilateral pentagon. Clearly, the so-called "triangular" sternum found in most buthids is also five-sided as well, except the two anterior sides forming the apex are quite short, thus causing the plate to taper distally. The complete spectrum of degrees of this tapering from "equilateral pentagonal" to highly "triangular" is exhibited in many genera of buthoids. The same can be stated for the "transverse" sternum associated with the bothriurids, which has a very wide apex and short lateral sides, however, again, exhibiting five sides. Of a particular interest here, Kjellesvig-Waering (1986: 15), when reflecting on the current family diversity of Recent scorpions, endorsed at most three Recent scorpion families, based entirely on these three forms, disregarding other characters. This restricted stance is strange taken in the context of Kjellesvig-Waering's general observation that all sterna are in fact pentagonal, which seemingly reduces the importance of the three shapes – and yet, he considered these three shapes important enough for family distinctions. Stockwell (1989), in a somewhat bemused tone stated that if one accepted Kjellesvig-Waering's statements literally (i.e., taking these "shapes" and overall proportions verbatim), we would have to create a new family for the euscorpiid *Troglocormus* due to its very elongated sternum, place *Caraboctonus* with the bothriurids, and remove genera with "pentagonal" sterna from the Buthidae. But after stating this, as if the differences were not important, Stockwell then provides all sorts of cladistic reasons for these "seemingly contradictions" thus giving weight to their importance – i.e., as if these "differences" were important in a cladistic sense. We argue here that these differences are not important whatsoever since they don't involve fundamental changes in sternum structure, but only reflect instances of subtle variability of the pentagonal shape. [As a side note, it is clear that the elongated sternum found in the scorpion *Troglocor-*

mus is due, in part, to its cave adaptation, since the species in general is somewhat elongated. In addition, members of this euscorpiid subfamily, Scorpiopinae, all have sterna that are longer than wide, *Troglocormus* being just a more exaggerated form (see Soleglad & Sissom, 2001: 108-109.).].

The credibility of the buthid "triangular" sternum as a significant taxonomic character is further strained by Petrunkevitch's (1916) observation that early instar *Centruroides* species have pentagonal sterna, as opposed to the more standard "triangular" form as seen in adults. Pavlovskij (1924) confirmed and illustrated the same shape shift in newborn versus first instars of *Hottentotta eminii* (Buthidae). This fact was interpreted by Petrunkevitch (1916) as a manifestation of Haeckel's "law" of recapitulation, and the pentagonal sternum shape as a primitive condition (character state). Recapitulation theories notwithstanding, this observation undermines the importance of the overall sternum shape character by indicating a possible dependence on ontogenetic influences. Sissom (1990: 89) mentioned that most buthids have a "subtriangular" sternum but *all* first-instar buthids have a "subpentagonal" sternum, and this characteristic persists in the adult in *Akentrobuthus*, *Butheoloides*, *Charmus*, *Karasbergia*, *Microtityus*, and some *Orthochirus*. Similarly, first-instar bothriurids also have a subpentagonal sternum, not exhibiting the exaggerated "transverse" form as found in adults (personal observation of *Bothriurus* by Luis Acosta).

Paradoxically, reducing the sternum characterization to simple "shape" caused Birula (1917a, 1917b) to create two levels of family-group taxa for the East Indian genus *Charmus* Karsch. So important was the basic shape character (a "pentagonal, wider than length" sternum) that Karsch (1879b: 104), describing a new genus, placed it under the group "Jurini" side-by-side with *Uroctonus* and *Scorpiops*, completely overriding other characters. The genus was correctly placed in Buthidae by Pocock (1893) and Kraepelin (1899). Birula (1917a: 160, 186), on the other hand, kept *Charmus* in Vaejovidae, but glaring discrepancies in many other characters forced Birula to accommodate it under a special higher taxon – first a subfamily Charminae (Birula, 1917a: 193), and later even a special "tribe Charmaria" (Birula, 1917b: 57), an intermediate taxon between family and subfamily ranks (not equivalent to the modern rank of tribe, between subfamily and genus). This subfamily name was never used by subsequent researchers (Fet & Lowe, 2000: 55, 57), but technically is still an available under Buthidae, where *Charmus* justly belongs (Werner, 1934; Sreenivasa-Reddy, 1966; Fet & Lowe, 2000; Lourenço, 2002). Similarly, Mello-Leitão (1934) described *Physoctonus physurus* which he placed in the family Vaejovidae. As it turned out, the scorpion was an immature species of *Rhopalurus* (Francke, 1977). Clearly, the so-called "pentagonal" sternum shape ex-

hibited in these two genera, *Charmus* and *Physoctonus*, was the cause for these results, in one case a species of small size, and in the other, an immature specimen.

Thus, the characterization of the sternum in scorpion systematics has not changed since the late 19th century, with three basic sternum shapes widely accepted then as well as now. Due to the many inconsistencies encountered in this seemingly simple and basic scorpion structure, we decided to reanalyze the sternum in detail ignoring the current characterizations involving overall shape and general proportions. In this study we have analyzed the structure of the scorpion sternum from both an external and (for the first time) internal perspective. All major Recent scorpion groups have been analyzed, involving 89 genera. As it turns out, many of the important external substructures identified and described in this paper are further supported and elucidated by their internal counterparts. For the buthoids and bothriurids we propose a set of derivations that, in part, explain their unique form within the fundamental sternum structure. We also calculated a small set of morphometric ratios that, as we believe, best support the observations and hypothesis presented herein. Finally, we discuss the phylogenetic and taxonomic ramifications of this new perspective on the scorpion sternum.

Methods & Material

In this paper we refer to several taxonomic groupings that are not yet well-justified or officially established, though, in some cases, have been referenced or alluded to in other sources. For convenience, we use the term "buthoid" to refer to the two scorpion families, Buthidae and Microcharmidae. Lourenço (2001a) placed these families in the superfamily Buthoidea; however, the issue of scorpion superfamilies has not yet been discussed in detail. In Soleglad & Sissom's (2001: 68-70, 87-88) revision of family Euscorpiidae, it was suggested that the genera *Anuroctonus* (currently in family Iuridae) and *Belisarius* (family Troglotayosicidae) both showed a closer affinity with the South American family Chactidae. The possible affiliation of *Anuroctonus* with Chactidae was based on a large-scale preliminary cladistic analysis, while the possible affiliation of *Belisarius*, used as an outgroup for Euscorpiidae, was demonstrated, in part, by Soleglad & Sissom (2001). We follow the suggested grouping in this paper in the comparative morphology and morphometric analyses. We do not yet make a formal transfer of *Anuroctonus* and *Belisarius* to Chactidae; however, it is our opinion that to leave these two genera in their current families would artificially skew the results of these analyses. Finally, although the superfamily and genus-family issues just discussed are not officially established (Fet et al., 2000), their delinea-
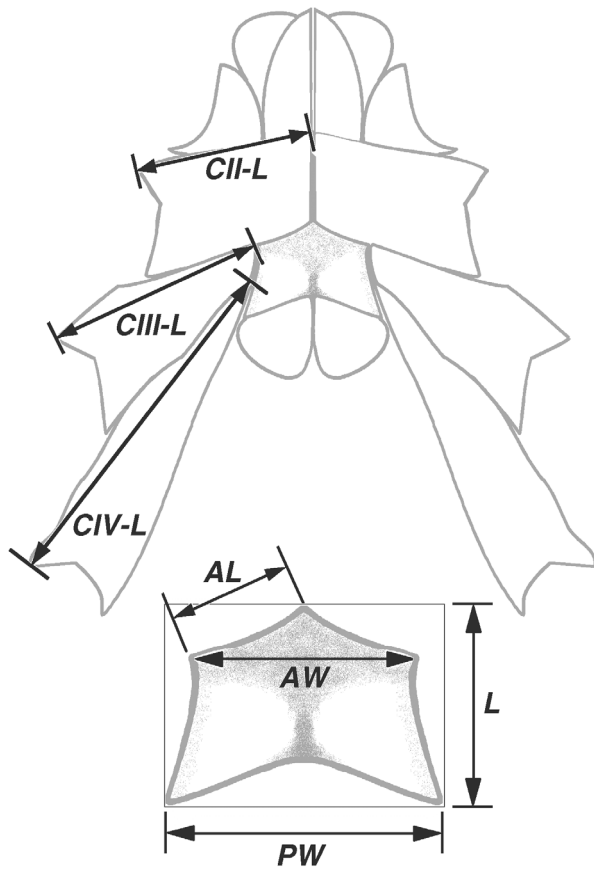
Figure 1: Methods of measurement of the sternocoxal area. *CII-L* = leg coxa II length, *CIII-L* = leg coxa III length, *CIV-L* = leg coxa IV length, *L* = sternum length, *PW* = sternum posterior width, *AW* = sternum apex width, *AL* = sternum apex lateral side length.

tion is now under work based on morphological and molecular data (Soleglad & Fet, in progress).

Sternum Removal

We removed the sternum from 46 genera representing all major Recent scorpion groups (see **Material Examined** below for actual genera dissected). Each sternum was removed by detaching its apex from leg coxae II by cutting in the deep grove separating the coxal plates and sternum. The same technique was employed on the lateral edges of the sternum separating it from the distal internal aspects of leg coxae III and IV. The posterior edge of the sternum was separated from the bordering genital operculum by cutting below the interconnecting pleural membrane at a slight downward angle. The internal side of the sternum was then cleansed of membrane and soft tissue with small forceps. In some cases, this last step was expedited by first soaking the sternum in clove oil as recommended for hemispermato-

phore cleansing. The soft tissue on the sternum, however, is thicker and much more coarse than the very delicate material surrounding the chitinous parts of the hemispermatophore so the technique gave only modest results. Since most sterna in general are composed of thick cuticle, they can withstand the relative abuse of careful forceps cleaning. This is particularly true of sterna from large specimens.

Morphometrics

Seven measurements of the sternocoxal area were taken from the material examined in this study (100 sets of measurements in all): three leg coxae length measurements, coxae II, III, and IV (referred to in this study as *Coxa II$_L$*, *Coxa III$_L$*, and *Coxa IV$_L$*) and four sternum measurements were taken, length (*Sternum$_L$*), apex lateral side length (*Sternum$_{AL}$*), apex width (*Sternum$_{AW}$*), and posterior width (*Sternum$_{PW}$*). The coxa length measurement is the linear distance from the extreme inner aspect to the extreme outer aspect taken along the anterior edge. Sternum length is calculated by constructing the tightest fitting rectangle that contains the sternum and measuring the vertical length of the rectangle. The apex lateral side length is the linear distance from the apex vertex to the lateral corner that is defined by the anterior inner aspect of leg coxa III. The two sternum widths are calculated as follows: the apex width is the horizontal distance between the two apex lateral corners, and the posterior width is the horizontal width of the rectangle. See Fig. 1 for the exact method of measurement. Five morphometric ratios were constructed from these seven measurements: *Coxa III$_L$/Coxa II$_L$*, *Coxa IV$_L$/Coxa II$_L$*, *Coxa II$_L$/Sternum$_{AL}$*, *Sternum$_{PW}$/Sternum$_{AW}$*, and *Sternum$_L$/Sternum$_{PW}$*.

Abbreviations

List of depositories: AMNH, American Museum of Natural History, New York, New York, USA; CAS, California Academy of Science, San Francisco, California, USA; GL, Personal collection of Graeme Lowe, Philadelphia, Pennsylvania, USA; FK, Personal collection of František Kovařík, Prague, Czech Republic; LP, Personal collection of Lorenzo Prendini, New York, New York, USA; MES, Personal collection of Michael E. Soleglad, Borrego Springs, California, USA; MHNG, Museum d'Histoire Naturelle de Geneve, Geneva, Switzerland, NHMW, Naturhistorisches Museum, Vienna, Austria; NMB, Naturhistorisches Museum, Basel, Switzerland; VF, Personal collection of Victor Fet, Huntington, West Virginia, USA; USNM, United States National Museum (Smithsonian Institution), Washington, DC, USA; WDS, Personal collection of W. David Sissom, Canyon, Texas, USA.

Material Examined

We examined the sternocoxal area of a large set of taxa representing all major groups of Recent scorpions (only family Heteroscorpionidae was not studied). The following scorpions (well over 100 species spanning 89 genera) were examined in this study for either structure analysis, morphometrics, internal dissection and/or illustration. If the sternum was dissected for internal examination it is noted. See this section for locality data of species level illustrations.

Pseudochactidae (1 genus): *Pseudochactas ovchinnikovi* Gromov, 1998, Babatag, Uzbekistan (Figs. 2, 3 and 14), ♂ (VF) [dissected].

Buthidae (29 genera): *Alayotityus nanus* Armas, 1973, Santiago, Cuba (Fig. 3), (VF); *Androctonus bicolor* Ehrenberg, 1828, Lhav, Israel, ♂ (MES); *Anomalobuthus rickmersi* Kraepelin, 1900, Bukhara, Uzbekistan (Fig. 4), (VF); *Apistobuthus pterygocercus* Finnegan, 1932, Oman (Fig. 16), (VF) [dissected]; *Babycurus exquisitus* Lowe, 2000, Oman, ♂ (NMB); *Buthacus yotvatensis* Levy, Amitai & Shulov, 1973, Abu Dhabi, United Arab Emirates, ♂ (VF); *Centruroides exilicauda* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico (Figs. 4 and 18), ♀ (MES) [dissected]; *Centruroides hentzi* (Banks, 1910), Panama City, Florida, USA, ♂ (MES); *Compsobuthus matthiesseni* (Birula, 1905), Baghdad, Iraq (Fig. 4), (VF); *Grosphus hirtus* Kraepelin, 1901, Tamatave Province, Perinet, Madagascar (Fig. 4), ♀ (MES); *Hottentotta minax* (L. Koch, 1875), Eritrea, ♂ (VF) [dissected]; *Isometrus maculatus* (DeGeer, 1778), Rime Road, Singapore (Fig. 4), ♂ (VF); *Isometrus* sp., Papua New Guinea, ♀ (MES) [dissected]; *Karasbergia methueni* Hewitt, 1913, Uapur Upington, South Africa (Fig. 3), ♂ (LP); *Kraepelinia palpator* (Birula, 1903), Badghyz, Turkmenistan, ♀ (VF); *Leiurus quinquestriatus* (Ehrenberg, 1828), Saudi Arabia, (VF); *Liobuthus kessleri* Birula, 1898, Chardara, Kazakhstan (Fig. 4), (VF); *Lychas* sp., Viti Levu, Fiji, ♀ (MES) [dissected]; *Lychas* sp., Indonesia (Fig. 4), (VF); *Mesobuthus caucasicus* (Nordmann, 1840), Chardara, Kazakhstan (Figs. 2, 4 and 17), ♀ (VF) [dissected]; *Microbuthus* sp., Jabal Bani Jabir, Oman (Fig. 4), ♀ (GL); *Microtityus jaumei* Armas, 1974, Santiago, Cuba (Fig. 3), (VF); *Odontobuthus* sp., Oman, ♀ (GL); *Orthochirus scrobiculosus* (Grube, 1873), Israel (Fig. 4), (MES); *Parabuthus* sp., Kenya (Fig. 3), (VF) [dissected]; *Paraorthochirus glabrifrons* (Kraepelin, 1903), Oman, ♀ (GL); *Polisius persicus* Fet, Capes & Sissom, 2001, Zahedan, Iran, ♂ (USNM); *Razianus zarudnyi* (Birula, 1903), Gachsaran, Fars, Iran (Fig. 4), (VF); *Rhopalurus junceus* (Herbst, 1800), Camaquey, Sibanidi, Cuba (Figs. 4 and 19), ♀ (VF) [dissected]; *Tityus nematochirus* Mello-Leitão, 1940, Bucaramango, Colombia (Figs. 36-37), ♂ (MES) [dissected]; *Uroplectes vittatus* (Thorell, 1876), Doddiebum, Zimbabwe, ♂ (VF); *Vachoniolus globimanus* Levy, Amitai & Shulov, 1973, Oman, ♂ (VF).

Microcharmidae (1 genus): *Microcharmus hauseri* Lourenço, 1996, Lokobe Natural Reserve, Île Nosy Be, Madagascar (Fig. 3), holotype ♂ (MHNG).

Chaerilidae (1 genus): *Chaerilus celebensis* Pocock, 1894, Luzon, Philippines (Fig. 3), ♂ (WDS); *Chaerilus petrzelkai* Kovařík, 2000, Saigon Province, Vietnam, (Fig. 3), holotype ♀ (FK); *Chaerilus variegatus* Simon, 1877, Indonesia (Figs. 15, 34-35), ♂ (MES) [dissected].

Iuridae (6 genera): *Anuroctonus phaiodactylus* (Wood, 1863), Beaver Co., Utah (Fig. 6), USA, ♂ (MES); *Anuroctonus* sp., Anza-Borrego Desert State Park (ABDSP), California, USA, ♂ (MES) [dissected]; *Calchas nordmanni* Birula, 1899, Antalya, Turkey (Fig. 2 and 8), ♀ (NHMW); *Caraboctonus keyserlingi* Pocock, 1893, Chili (Fig. 8), ♂ (MES) [dissected]; *Hadruroides charcasus* (Karsch, 1879), Peru, ♂ (MES); *Hadruroides maculatus* (Thorell, 1876), Huancayo, Peru (Fig. 8), ♀ (MES) [dissected]; *Hadrurus arizonensis* Ewing, 1928, Maricopa Co., Arizona, USA, (MES) [dissected]; *Hadrurus aztecus* Pocock, 1902, Tehuacan, Puebla, Mexico, ♂ (MES); *Hadrurus concolor* Stahnke, 1969, Santa Rosalia, Baja California Sur, Mexico (Figs. 8, 21, and 38-39), ♀ (MES) [dissected]; *Iurus dufoureius* (Brullé, 1832), Turkey (Figs. 8 and 20), ♂ (MES) [dissected].

Bothriuridae (7 genera): *Bothriurus araguayae* Vellard, 1934, Minas Gerais, Brazil, ♀ (VF); *Bothriurus burmeisteri* Kraepelin, 1894, Gobernador Costa, Chubut, Argentina (Figs. 5 and 40-41), (VF) [dissected]; *Brachistosternus ehrenberghii* (Gervais, 1841), Tarapaca Province, Valle de Azapa, Chile, ♂ (VF); *Brachistosternus* sp., Antofagasta Province, Rio Loa, Chile (Fig. 25), (VF) [dissected]; *Centromachetes pocockii* (Kraepelin, 1894), Lebu, Arauco, Chile (Fig. 5), (VF) [dissected]; *Cercophonius squama* (Gervais, 1843), Engadine, Sidney, Australia (Fig. 2), ♀ (VF) [dissected]; *Cercophonius* sp., Mt. Field National Park, Tasmania, Australia (Fig. 5), (USNM); *Orobothriurus* sp., Ancash Dept., Laguna Llagannco, Peru, (MES) [dissected]; *Phoniocercus pictus* Pocock, Valdivia Nancul, Fundo El Linque, Chile, ♀ (VF) [dissected]; *Phoniocercus sanmartini* Cekalovic, 1973, Concepcion Province, Estero Nonguen, Chile, (VF); *Urophonius granulatus* Pocock, 1898, Ultima Esperanza, Laguna Amarga, Chile, ♂ (VF) [dissected].

Scorpionidae (4 genera): *Heterometrus longimanus* (Herbst, 1800), Mindanao, Philippines (Fig. 22), ♂ (MES) [dissected]; *Heterometrus petersii* (Thorell, 1876), Palawan, Philippines, ♂ (USNM); *Opistophthalmus* sp., Johannesburg, South Africa (Fig. 5), ♀ (MES); *Pandinus imperator* (C. L. Koch, 1841), ♀ (MES); *Scorpio maurus* Linnaeus, 1758, Tel-Yezucham, Israel (Fig. 5), ♀ (MES) [dissected].

Diplocentridae (5 genera): *Bioculus comondae* Stahnke, 1968, Loreto, Baja California Sur, Mexico, ♂ (MES) [dissected]; *Cazierius gundlachii* (Karsch, 1880), San Juan, Santiago de Cuba, Cuba, ♂ (VF); *Didymocentrus leseurii* (Gervais, 1844), Martinique, ♀ (VF); *Diplocentrus ochoterenai* Hoffmann, 1931, Oaxaca, Mexico (Fig. 5 and 23), ♀ (MES) [dissected]; *Diplocentrus whitei* (Gervais, 1844), Cuatro Cienegas, Coahuila, Mexico, ♂ (MES); *Nebo hierichonticus* (Simon, 1872), Haifa, Israel, ♀ (VF).

Ischnuridae (4 genera): *Cheloctonus* sp., St. Lucia, Kwazula, Natal (Fig. 5), ♀ (VF) [dissected]; *Hadogenes troglodytes* (Peters, 1861), Johannesburg, South Africa (Fig. 5), ♀ (MES) [dissected]; *Liocheles* sp., Papua New Guinea (Figs. 5), ♀ (MES) [dissected]; *Liocheles* sp., Guadalcanal, Solomon Islands, ♂ (MES); *Opisthacanthus lepturus* (Beauvois, 1805), Canal Zone, Panama (Figs. 5 and 24), ♀ (MES) [dissected].

Urodacidae (1 genus): *Urodacus manicatus* (Thorell, 1876), Australia (Fig. 5), (VF) [dissected].

Hemiscorpiidae (1 genus): *Hemiscorpius maindroni* (Kraepelin, 1900), Wadi Bani Kharus, Oman (Fig. 5), ♀ (GL), Wadi Mistal, Oman, ♂ (GL).

Euscorpiidae (9 genera): *Alloscorpiops lindstroemii* (Thorell, 1889), Tak Province, Umphang, Thailand, ♀ (CAS); *Chactopsis insignis* Kraepelin, 1912, Loreto, Peru (Fig. 6), ♀ (MNHN); *Euscorpiops binghamii* (Pocock, 1893), Misty Hollow, Dawna Hills, Burma (Fig. 6), ♀ (WDS); *Euscorpius flavicaudis* (DeGeer, 1778), Banyuls, France (Fig. 6), ♂ (MES); *Euscorpius italicus* (Herbst, 1800), Agarone, Ticino, Switzerland (Fig. 27), ♂ (MES) [dissected]; *Megacormus gertschi* Díaz Nájera, 1966, Zacualtipan, Hidalgo, Mexico (Fig. 6 and 26), ♀ (MES) [dissected]; *Neoscorpiops tenuicauda* (Pocock, 1894), Maharashtra, Bhimashankar, India, ♂ (CAS); *Plesiochactas dilutus* (Karsch, 1881), Portillo Nejapa, Oaxaca, Mexico, ♂ (AMNH); *Scorpiops tibetanus* Hirst, 1911, Lhasa, Tibet, ♂ (USNM); *Troglocormus willis* Francke, 1981, Cueva de la Llorona, Yerbabuena, Tamaulipas, Mexico (Fig. 6), ♀ (WDS).

Chactidae (7 genera): *Brotechactas delicatus* (Karsch, 1879), Grande Ile, French Guiana (Fig. 6), ♂ (MES); *Brotheas granulatus* Simon, 1877, Grande Île, French Guiana (Fig. 29), ♀ (MES) [dissected]; *Chactas* sp., Darien, Panama (Figs. 6 and 28), ♀ (MES) [dissected]; *Hadrurochactas schaumii* (Karsch, 1880), Petite Île, French Guiana (Fig. 6), ♂ (MES); *Nullibrotheas allenii* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico (Fig. 6), ♀ (MES) [dissected]; *Teuthraustes oculatus* Pocock, 1900, Latacunga, Ecuador (Fig. 6), ♀ (WDS); *Vachoniochactas* sp., Alto Rio Mavaca, Amazonas, Venezuela (CAS).

Troglotayosicidae (1 genus): *Belisarius xambeui* Simon, 1879, Vidra, Gerona, Catalunya, Spain (Fig. 6), ♀ (WDS).

Vaejovidae (10 genera): *Paravaejovis pumilis* (Williams, 1970), Ciudad Constitution, Baja California Sur, Mexico (Fig. 7), ♂ (MES); *Paruroctonus arnaudi* Williams, 1972, El Socorro, Baja California Norte, Mexico, ♂ (MES) [dissected]; *Paruroctonus silvestrii* (Borelli, 1909), ABDSP, California, USA (Fig. 7), (MES); *Pseudouroctonus reddelli* (Gertsch & Soleglad, 1972), Conal Co., Texas, USA (Fig. 7), ♀ (MES), Travis Co., Texas, USA, ♂ (MES) [dissected]; *Serradigitus joshuaensis* (Soleglad, 1972), ABDSP, California, USA (Fig. 7), (MES); *Serradigitus subtilimanus* (Soleglad, 1972), ABDSP, California, USA (Figs. 7 and 31), (MES) [dissected]; *Smeringurus aridus* (Soleglad, 1972), ABDSP, California, USA (Fig. 7), ♂ (MES); *Smeringurus mesaensis* (Stahnke, 1957), ABDSP, California, USA (Fig. 32), ♀ (MES) [dissected]; *Syntropis macrura* Kraepelin, 1900, Ensenada Marquer, Isla Carmen, Baja California Sur, Mexico (Fig. 7), ♀ (WDS); *Uroctonites huachuca* (Gertsch & Soleglad, 1972), Huachuca Mtns., Arizona, USA, ♂ (MES); *Uroctonus mordax* Thorell, 1876, Yosemite National Park, California, USA (Fig. 7), ♂ (MES) [dissected]; *Vaejovis eusthenura* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico (Fig. 7), ♀ (MES) [dissected]; *Vaejovis nitidulus* C. L. Koch, 1843, Cuicitlan, Oaxaca, Mexico (Fig. 7), ♀ (MES); *Vaejovis punctipalpi* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico (Figs. 7 and 30), ♀ (MES) [dissected]; *Vejovoidus longiunguis* (Williams, 1969), Los Bombas, Baja California Sur, Mexico (Fig. 7), (MES) [dissected].

Superstitioniidae (2 genera): *Superstitionia donensis* Stahnke, 1940, ABDSP, California, USA (Figs. 8, 9 and 33), ♀ (MES) [dissected], Peralta Canyon, Pinal Co., Arizona, USA, ♀ (MES) [dissected]; *Alacran tartarus* Francke, 1982, Huantla Sistema, Sotano de San Agustin, Oaxaca, Mexico (Figs. 8 and 10), ♀ (WDS).

Sternocoxal Configurations: An Overview

For Recent scorpions the overall sternocoxal configuration is identical across all families; in fact it is consistent within the infraorder Orthosterni (see Fig. 1). The sternum, roughly configured as a five-sided irregular pentagon, has its posterior side bordered by the anterior portion of the genital operculum; its two lateral sides are bordered by the internal distal aspects of leg coxae III and IV, and the two anterior lateral sides (forming the apex) are formed by leg coxae II, the extreme distal vertex of the apex splitting these coxae. The outside lateral vertices of the anterior apex edges are defined by the upper distal aspect of leg coxae III where they meet coxae II. This fundamental sternocoxal configuration present in all Recent scorpions is found in many fossil scorpion genera as well, dating as far back as the Lower Carboniferous (Lower Mississippian, 354 Ma, Kjellesvig-Waering, 1986). Kjellesvig-Waering (1986) reported
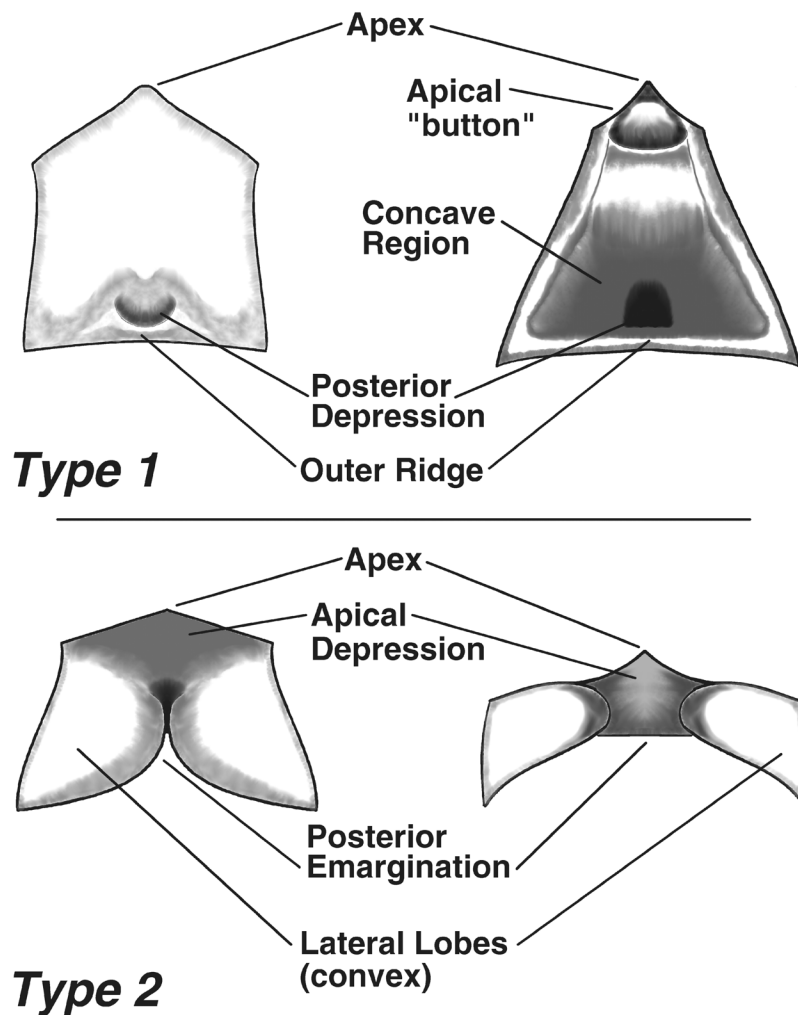
this configuration for genera occurring in all major infraorders he recognized: for Holosternina, genera *Allobuthus*, *Anthracoscorpius*, *Buthiscorpius*, *Eoctonus* (superfamily Eoctonoidea, Pennsylvanian, 323-290 Ma), and *Gigantoscorpius*, (superfamily Gigantoscorpionoidea, Lower Mississippian); for Meristosternina, genus *Palaeobuthus* (superfamily Palaeobuthoidea, Pennsylvanian); for Lobosternina, genera *Anthracochaerilus* (superfamily Anthracochaeriloidea, Mississippian), *Petaloscorpio*, *Pseudobuthiscorpius*, *Waterstonia* (superfamily Pseudobuthiscorpionoidea, Pennsylvanian); and for the Orthosternina (or Orthosterni of Jeram, 1994a), genus *Palaeopisthacanthus* (superfamily Scorpionoidea (not in the strict sense, as defined by Prendini, 2000), Pennsylvanian). Jeram (1994b: Fig. 4, G) also reported this fundamental sternocoxal configuration for the large scorpion *Pulmonoscorpius kirktonensis* (Lower Carboniferous) which he placed in Mesoscorpionina, a suborder recognized under Stockwell's (1989) classification. According to this classification, as modified by Jeram (1994b: Fig. 1), we see the fundamental sternocoxal arrangement stated as a synapomorphy for the orders Palaeoscorpiones + Scorpiones, distinguishing them from order Protoscorpiones. Jeram (1994b: 286) also referenced Stockwell (1989: 51-52) who suggested that the frequency of Palaeozoic scorpions having leg coxae IV abutting the genital operculum (a configuration presumably predating the fundamental arrangement discussed herein) may have been less than implied by Kjellesvig-Waering (1986). If this is true, then the fundamental arrangement seen in Recent scorpions may be even more prevalent in fossil scorpions than that discussed above.

We find the evolution of the two sets of maxillary lobes I and II (i.e., coxapophyses, Hjelle (1990: 12)) found in Recent scorpions to be quite interesting since their derivation may have occurred after the emergence of the sternocoxal configuration described above. The fundamental configuration found in these structures is the same across all Recent scorpions and is found in many fossil scorpion genera, again occurring as far back as the Lower Carboniferous period (this is amply illustrated in Kjellesvig-Waering, 1986). As evidenced by the fossil record and by examination of Recent scorpions, it is clear that the maxillary lobes derived directly from leg coxae I and II. Maxillary lobes I are the direct result of an external to internal vertical partitioning of leg coxae I, and lobes II are the result of a vertical lengthening of leg coxae II extending between coxae I. For Recent scorpions, the separation between maxillary lobes I and leg coxae I is well delineated, but the plates are not entirely separated. Maxillary lobes II and leg coxae II delineation is not as distinct as in lobes I, exhibiting variability, anywhere from a semi-deep groove to a subtle indentation. Again, as with lobes I, these lobes are not separated from leg coxae II. Three stages

of maxillary lobe development are illustrated in our Fig. 3 (after Kjellesvig-Waering, 1986) as well as in many other illustrations provided by Kjellesvig-Waering (1986). In Fig. 3 (*Gigantoscorpio*) we see leg coxae I and II aligned essentially in a horizontal position, maxillary lobes altogether absent; in Fig. 3 (*Waterstonia*) we see the extension of leg coxae II vertically separating, in part, leg coxae I, and with the deep lateral separation of leg coxa I, we can see the forming of maxillary lobes I, probably caused, in part, by the extension of coxae II; in Fig. 3 (*Palaeopisthacanthus*), maxillary lobes I are completely formed showing separation from leg coxae I, and maxillary lobes II are present as in the fundamental configuration, though they are not separated from leg coxae II. Note that, in the three fossil genera examples just discussed, no phylogenetic relationship is implied, except for gross timeline indications. *Gigantiscorpio* is found in Lower Carboniferous and the other two genera are found later in the Upper Carboniferous.

In Francke's (1986: Fig. 2) illustration of the sternocoxal area of *Typhlochactas cavicola* Francke we see that the maxillary lobes are not delineated from the leg coxae. Of a particular interest, leg coxae I and maxillary lobes I are fused. Since this illustration is somewhat small and not particularly well rendered, we cannot ascertain its validity with respect to this particular issue. Therefore we only mention it here since it is contrary to any other known Recent scorpion. The sternocoxal area of *Sotanochactas*, a typhlochactine, has a normal configuration, both maxillary lobes are distinct from the leg coxae (W. D. Sissom, personal communication). It should be also noted that the sternocoxal configuration is not discussed in any of the papers that define the seven species of the typhlochactines, although there are several excellent illustrations of the sternum proper.

The structure of the maxillary lobes has been used sparingly in Recent scorpion systematics, in particular, only for the genus *Chaerilus*. In this unique genus, maxillary lobes I are highly expanded distally forming a "spatulate" form (this particular term is attributed to Kjellesvig-Waering, 1986). Fig. 3 illustrates this form for two species of *Chaerilus*. Kjellesvig-Waering (1986: 232) had assigned the same form to the Carboniferous genus *Palaeopisthacanthus*, but Jeram (1994a: 524) disagreed with this interpretation, suggesting "… *Chaerilus*-like spatulate apophysis on the anterior coxa is probably part of the underlying pedipalpal coxa …". Assuming Jeram is correct, then *Chaerilus* is the only known taxon within the Orthosterni with this unique form, this feature thus being autapomorphic. Another interesting form involving maxillary lobes I is that reported, in part, by Stockwell (1989) and Prendini (2000), and observed by us in this study. Stockwell noted that in certain scorpionoids, maxillary lobes I extended beyond lobes II wrapping around their distal tips. Stockwell reported this phenomenon for certain scorpionoid genera

Apex

Apical
"button"

Concave
Region

Posterior
Depression

Outer Ridge

Type 1

Apex

Apical
Depression

Posterior
Emargination

Lateral Lobes
(convex)

Type 2

Figure 2: Fundamental sternum types illustrating special terminology (external view). Sternum *type 1*: *Pseudochactas ovchinnikovi* (left) and *Mesobuthus caucasicus*. Sternum *type 2*: *Calchas nordmanni* (left) and *Cercophonius squama*.

(in particular all four genera of Scorpionidae, and several ischnurids). We also noticed this same condition, in part, but only specifically for the ischnurids. It is clear that the scorpionids do not have this condition as reported by Stockwell. Prendini (2000: 62) also disagreed with Stockwell's observation, restricting this character to the ischnurids as well, considering it a synapomorphy for the family. The condition reported by Stockwell and Prendini can be stated as follows: maxillary lobes I are generally equally narrow at their base, midpoint and subterminal aspects, only narrowing at the extreme distal tips; the distal aspect usually extending beyond lobes II and sometimes curving inward, wrapping around the distal tips of lobes II. In contrast, for typical shaped maxillary lobes I, the basal aspect is quite narrow forming a highly rounded external midsection and smoothly curving inward meeting the distal tips of lobes II. We have observed this "narrowed" condition on the four ischnurid genera studied for this paper (Fig. 5), *Opisthacanthus*, *Hadogenes*, *Cheloctonus* and multiple species of *Liocheles*. The typical configuration was observed on all other non-ischnurid scorpionoid genera discussed and illustrated herein.

Sternum Structure Analysis

Above we addressed the problems with using the subtle shape differences of the sternum all presumably quantifying various degrees of an irregular pentagon. Although the three shapes traditionally used in scorpion systematics, in part, have merit in some small context, they do not actually reflect fundamental differences in sternum types since they don't deal with the actual structure. After review of sterna from over 100 Recent scorpion species representing all major scorpion groups, we have isolated two fundamental sternum types, which we refer to simply as sternum *type 1* and *type 2*. Below we present both external and internal characteristics in the definition of these two sternum types.

Definition of terms

Before defining these two fundamental sternum types, we introduce special terminology to describe this structure. In Figure 2 we illustrate two sterna for specific types, each depicting the wide spectrum of sternum forms exhibited within each type. For *type 1* sterna,

Pseudochactas and the buthid *Mesobuthus* provide an excellent contrast, similarly, *type 2* sterna are well represented by the iurid *Calchas* and the bothriurid *Cercophonius*.

External Aspect

- *Apex:* the anterior (distal) area of the sternum. Found in both sternal types.

- *Posterior depression:* a small to large variable shaped depression formed minimally as a "dimple" to a deep depression, found on posterior portion of the sternum, but always above the extreme posterior edge. Found in sternal *type 1*.

- *Outer ridge:* a narrow ridge that partially circumscribes the sternum posteriorly and sometimes laterally in a posterior to anterior direction. Found in sternal *type 1*.

- *Concave region:* a variable sized medially symmetric concave area enclosed within the outer ridge. Sometimes found in sternal *type 1*.

- *Median furrow (not illustrated):* a narrow to wide median depression that extends from the posterior depression anteriorly towards the apex, forming the strict medial portion of the *concave region*. Sometimes found in sternal *type 1*.

- *Apical "button":* a small slightly convex area of the apex formed anteriorly of the concave region. Sometimes found in sternal *type 1*.

- *Posterior emargination:* A deep vertical median groove found on the posterior half of the sternum subdividing the sternum into two highly convex *lateral lobes*. Found in sternal *type 2*.

- *Lateral lobes:* two rounded highly convex projections found on the proximal half of the sternum; formed by the posterior emargination. Found in sternal *type 2*.

- *Apical depression:* the variable depressed area formed at the apex extending to the anterior edge of the lateral lobes. Variable in sternal *type 2*.

Internal Aspect

- *Posterior depression process:* a rounded projection of variable size and development that internally forms the convex aspect of the posterior depression. Found in sternal *type 1*.

- *Posterior emargination processes*: two projections of variable size and development that internally form the internal posterior edges of the lateral lobes caused by the posterior emargination. Found in sternal *type 2*.

Fundamental sternum types

Sternum type 1: is characterized as follows: **always with a posterior depression that does *not* bisect the posterior edge of the sternum**. The posterior depression, of variable size and development, is always bordered posteriorly by an outer ridge. Medially a concave region may be found emanating from the posterior depression, sometimes narrowing anteriorly into a median furrow. The apex is of various size and form, sometimes exhibiting a modest apical depression or a slightly convexed 'button". The posterior depression is represented *internally* by a single rounded protruding process of variable size and development. Sternum has **five** sides, exhibiting forms ranging from equilateral pentagonal, subpentagonal, to narrowed elongated pentagonal (the so-called "triangular" shape). Sternum *type 1* is hypothesized here as a "primitive" form, attributed to the palaeopisthacanthids, pseudochactids, chaerilids, and the buthoids.

Sternum type 2: is characterized as follows: **always with posterior emargination and convex lateral lobes**. An apical depression is always present, though exhibiting various degrees of deepness depending on the form and development of the lateral lobes. The posterior emargination is represented *internally* by two variable sized and developed protruding processes, each emanating from the inner posterior aspect of the lateral lobes. Sternum has **six** sides, the posterior edge *bifurcated* by the posterior emargination; shape proportion is variable, from highly elongated, equilateral, to much wider than long (the so-called transverse shape). Sternum *type 2* is hypothesized for all scorpions exhibiting Type C orthobothriotaxy, the so-called "non-primitive" Recent scorpions.

Sternum types in Recent scorpions

Several sternocoxal configurations are illustrated in Figs. 3-8, showing examples across all major groups of Recent scorpions. The two sternal types described above
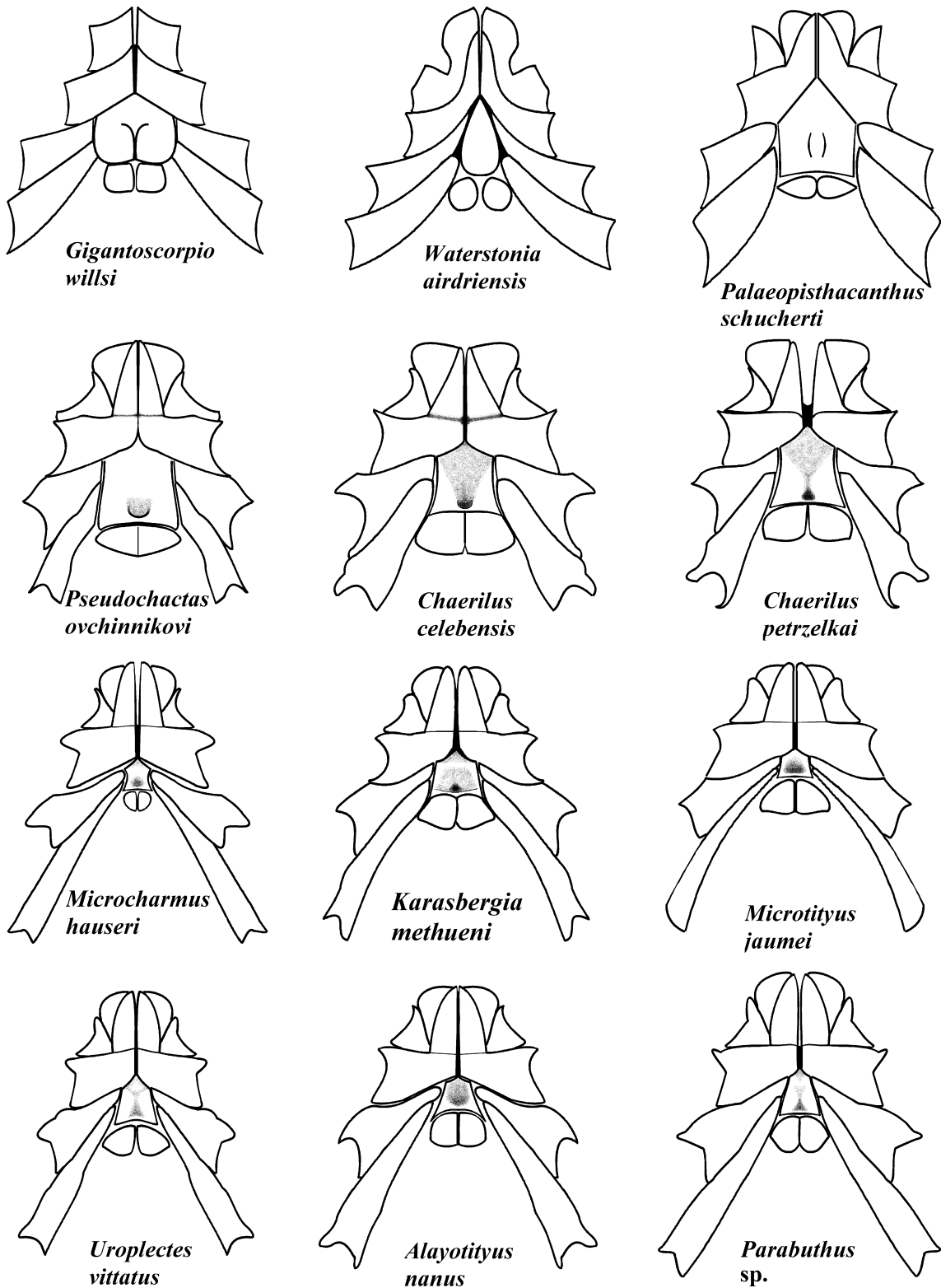
Figure 3: Sternocoxal area of fossil (Lower and Upper Carboniferous, after Kjellesvig-Waering, 1986) and Recent scorpion genera (*type 1* sterna), Pseudochactidae, Chaerilidae, Buthidae, and Microcharmidae. *Gigantoscorpio willsi* (Holosternina), Lower Mississippian (354-339 Ma), *Watersonia airdriensis* (Lobosternina), Lower Pennsylvanian (323-307 Ma), *Palaeopistha-canthus schucherti* (Orthosternina), Upper Pennsylvanian (307-290 Ma).
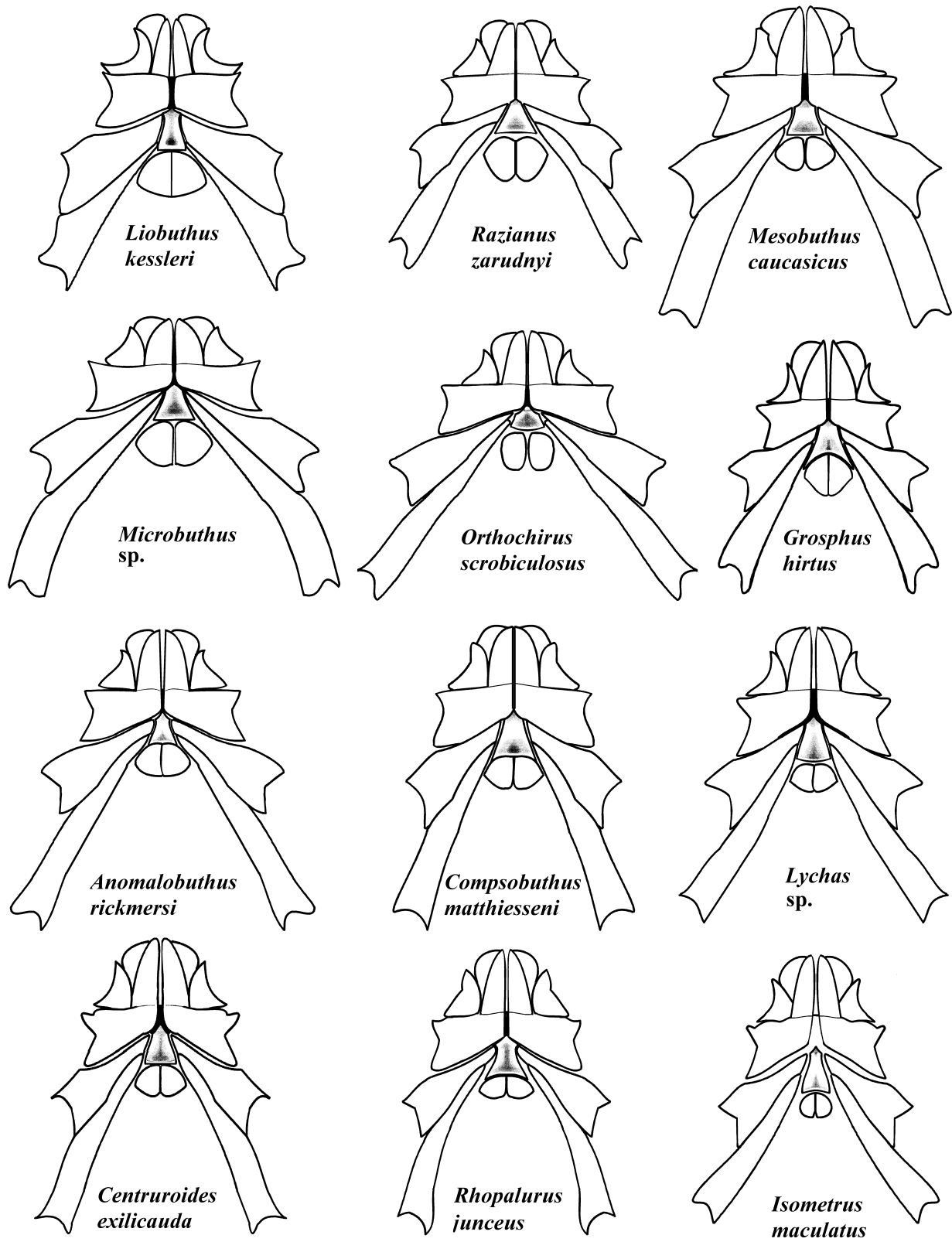
Figure 4: Sternocoxal area of Recent scorpion genera (*type 1* sterna), Buthidae continued.

are quite evident by carefully inspecting the external aspect of these sterna. Figs. 3-4 illustrate *type 1* sterna and Figs. 5-8 show *type 2* sterna. In these illustrations the leg coxae, maxillary lobes and genital operculum are shown diagrammatically as outlines whereas the sternum is shaded in order to depict its finer three-dimensional structure.

Type 1 sterna: In Figs. 3-4 we illustrate the sternocoxal areas of the three groups of Recent scorpions representing *type 1* sterna: the pseudochactids, the chaerilids and the buthoids (eighteen genera including *Microcharmus*). Apparent from these figures and a common denominator is the posterior depression accompanied by a small to somewhat significant outer ridge, found at least on the medial posterior aspect. In all cases the posterior depression does not bisect the posterior edge of the sternum. The shape and overall size of this posterior depression is varied across the genera illustrated. For example, *Pseudochactas* (Fig. 3) has the most reduced depression without any trace of an accompanying concave region or median furrow. The chaerilids (two species of *Chaerilus* illustrated, Fig. 3) also have a narrow posterior depression but it is considerably deeper than in *Pseudochactas*, plus it widens anteriorly, thus providing a subtle wide concave region for this portion of the sternum. In contrast, the sternum in *Pseudochactas* is essentially flat. For these two genera, the sternum, pentagonal in shape, is a little longer than wide. In the buthoids, the posterior depression is quite varied, wide and somewhat short on genera *Karasbergia* (Fig. 3), *Microtityus* (Fig. 3), *Mesobuthus* (Fig. 4) and *Compsobuthus* (Fig. 4). For genera *Microbuthus* (Fig. 4), *Centruroides* (Fig. 4), *Rhopalurus* (Fig 4) and *Tityus* (Figs. 36-37), the posterior depression is longer extending further anteriorly. We attempted to obtain as many buthoid genera as possible that were attributed with "pentagonal sterna", but are missing such genera as *Charmus* and *Akentrobuthus*. However, we were able to obtain some fairly rare genera that do reflect this sternum shape. In particular, *Karasbergia* and *Microcharmus* are noteworthy. The genus *Microtityus* is also important since it complies with the characteristics associated with this form of buthoid sternum based on other characters and morphometrics discussed in detail elsewhere.

Of special interest here is the possible association of small buthoids and the "pentagonal sternum". Since the "pentagonal" sternum is shared by juvenile buthids (Petrunkevitch, 1916; Sissom, 1990), maybe size is a contributing factor to this shape across all ontogenetic stages. *Microcharmus*, *Karasbergia, Akentrobuthus*, and *Microtityus* are indeed small scorpions, all under 25 mm or smaller (*Microcharmus* under 16 mm) in total length, and they do exhibit the most exaggerated "pentagonal sterna". Genus *Charmus* whose sternum is depicted as "pentagonal" is also a small scorpion (adults, 15 to 30 mm; Sreenivasa-Reddy, 1966; Lourenço, 2002). How-
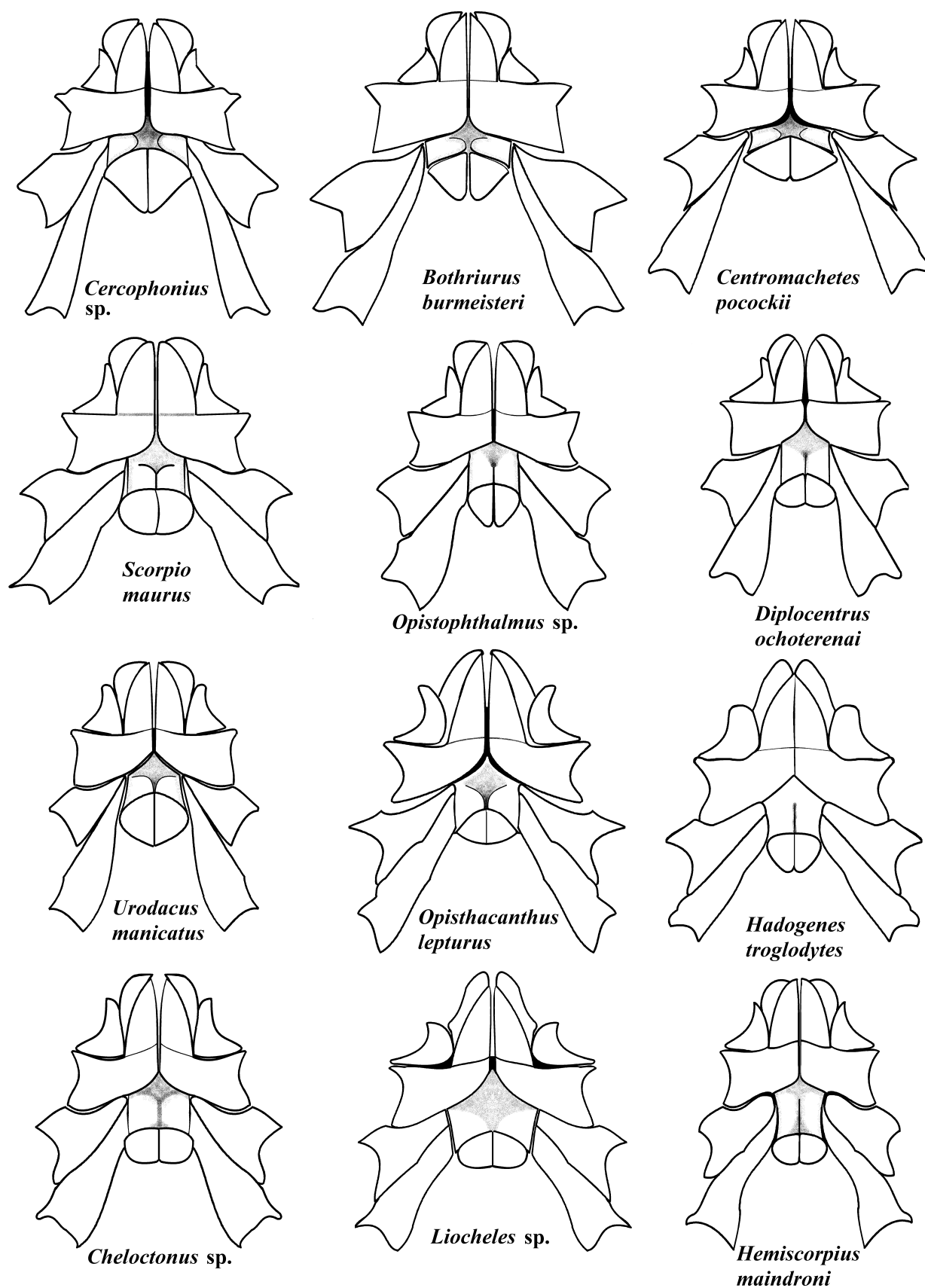
ever, "small size" is not an equivalency with "pentagonal" sterna, since we see that the very small buthid genera *Microbuthus* and *Orthochirus* do not have "pentagonal sterna". In fact, *Microbuthus* (Fig. 4) has one of the more "triangular" sterna based on other analysis presented elsewhere in this paper and in *Orthochirus* (Fig. 4), sternum is essentially equilateral, a "true triangle".

Also of note is the apparent elongation of leg coxae III and IV which is quite evident in most of the buthoid genera illustrated in Figs. 3-4. This elongation is conspicuous when compared to the pseudochactids and chaerilids (Fig. 3) as well as most *type 2* sterna scorpions (Figs. 5-8). We suggest here that this elongation is caused, in part, by the narrowing of the buthoid sternum thus the coxae III and IV must extend farther inward to abut the sternum. We quantify this elongation elsewhere in this paper using morphometric ratios.
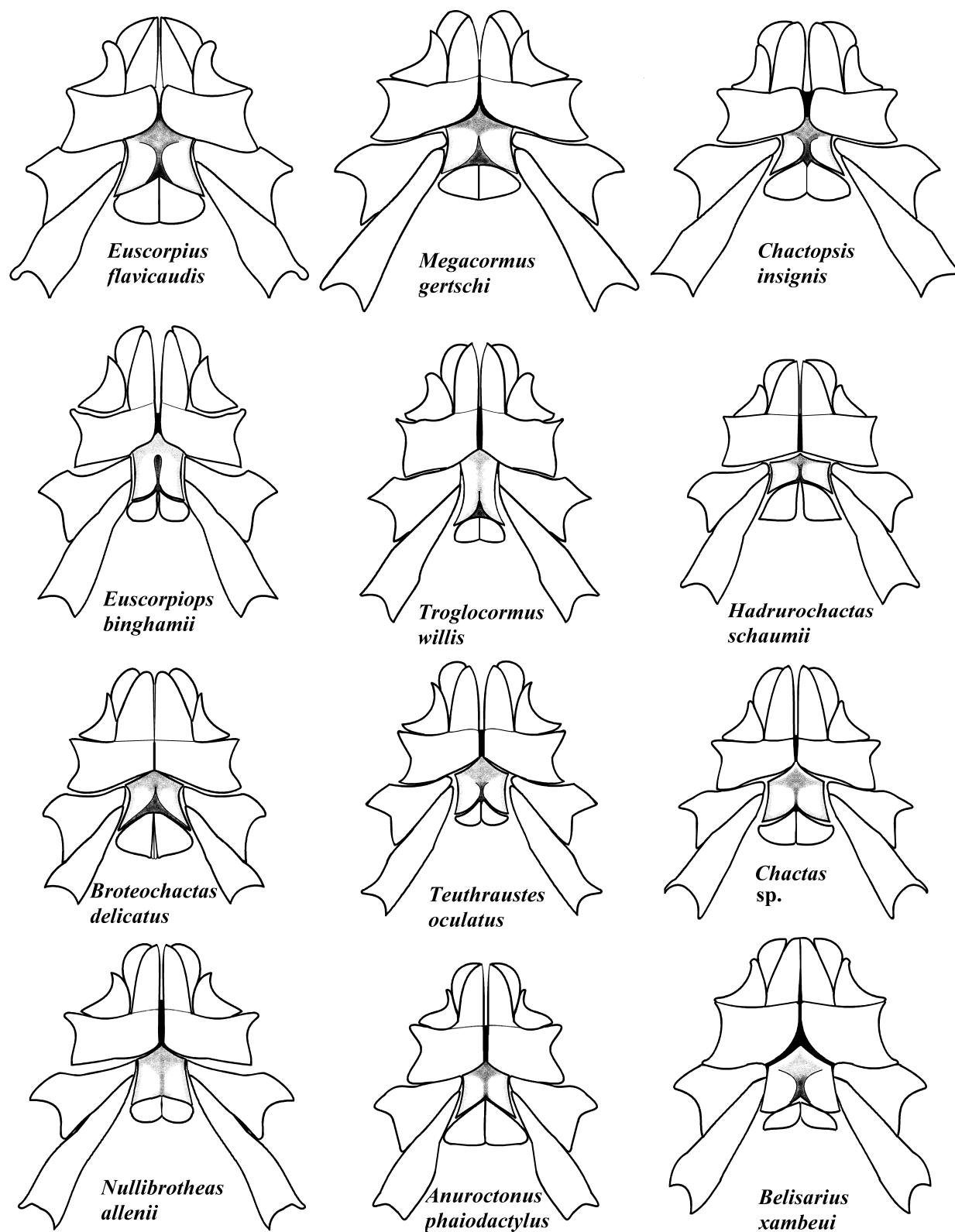
Type 2 sterna: The great diversity in size and overall proportions of *type 2* sterna is apparent when examining the sternocoxal illustrations presented in Figs. 5-8. However, the fundamental characters specified for this sternum type are consistently found in all cases: each sternum's posterior edge is bifurcated by the posterior emargination forming two convex lateral lobes. The degree of depression of the sternum apex is directly a function of the extent of the convexity of the lateral lobes, the more convex the lobes, thus a more exaggerated posterior emargination, the deeper the apical depression. For example, in the iurids, especially genera *Hadrurus* and *Hadruroides* (Fig. 8), the apical depression is deep accompanied by highly convex lateral lobes. We will see later that this character is also supported by an internal examination of the sternum for these taxa. On the other extreme, especially in the genus *Liocheles* (Fig. 5), we see a very subtle posterior emargination, the lateral lobes slightly convexed, the apical depression minimal. Again, internal dissection also supports these observations.

The bothriurid sternum (three species shown in Fig. 5) is quite interesting: it is considerably wider than long, the apex is flattened, the lateral lobes internally are considerably separated, and their anterior edges are abutted by leg coxae II. This configuration is unprecedented in *type 2* sterna. As will be established below, this observation of the specialized modification of the lateral lobes is more significant than the simple statement of it being wider than long, which is also seen in other genera. The iurid *Caraboctonus* (Fig. 8) and superstitioniid *Superstitionia* (Fig. 8) also have sterna much wider than long, but the lateral lobes are not modified as in the bothriurids. Below we discuss these differences in detail, incorporating the internal sternum structure as well.

The proportions of the sternum length and widths are quite varied in *type 2* sterna but there is a tendency for longer than wide sterna in the euscorpiid subfamily Scorpiopinae (Fig. 6). In particular, *Troglocormus* has a

Figure 5: Sternocoxal area of Recent scorpion genera (*type 2* sterna), the Scorpionoidea.

Euscorpius flavicaudis

Megacormus gertschi

Chactopsis insignis

Euscorpiops binghamii

Troglocormus willis

Hadrurochactas schaumii

Broteochactas delicatus

Teuthraustes oculatus

Chactas sp.

Nullibrotheas allenii

Anuroctonus phaiodactylus

Belisarius xambeui

Figure 6: Sternocoxal area of Recent scorpion genera (*type 2* sterna), Euscorpiidae, Chactidae, and two genera with unclear placement: *Anuroctonus* (now in Iuridae) and *Belisarius* (now in Troglotayosicidae).
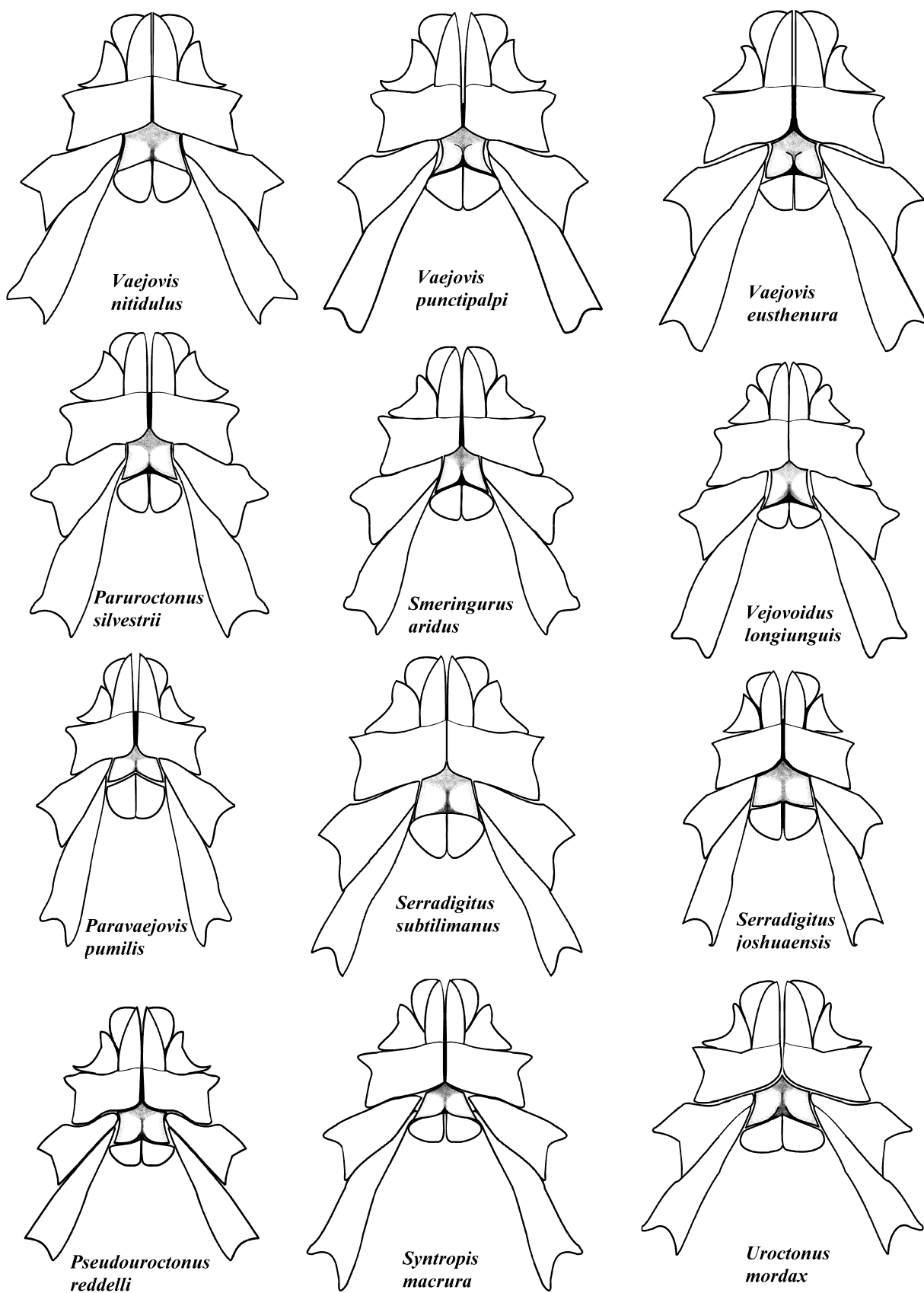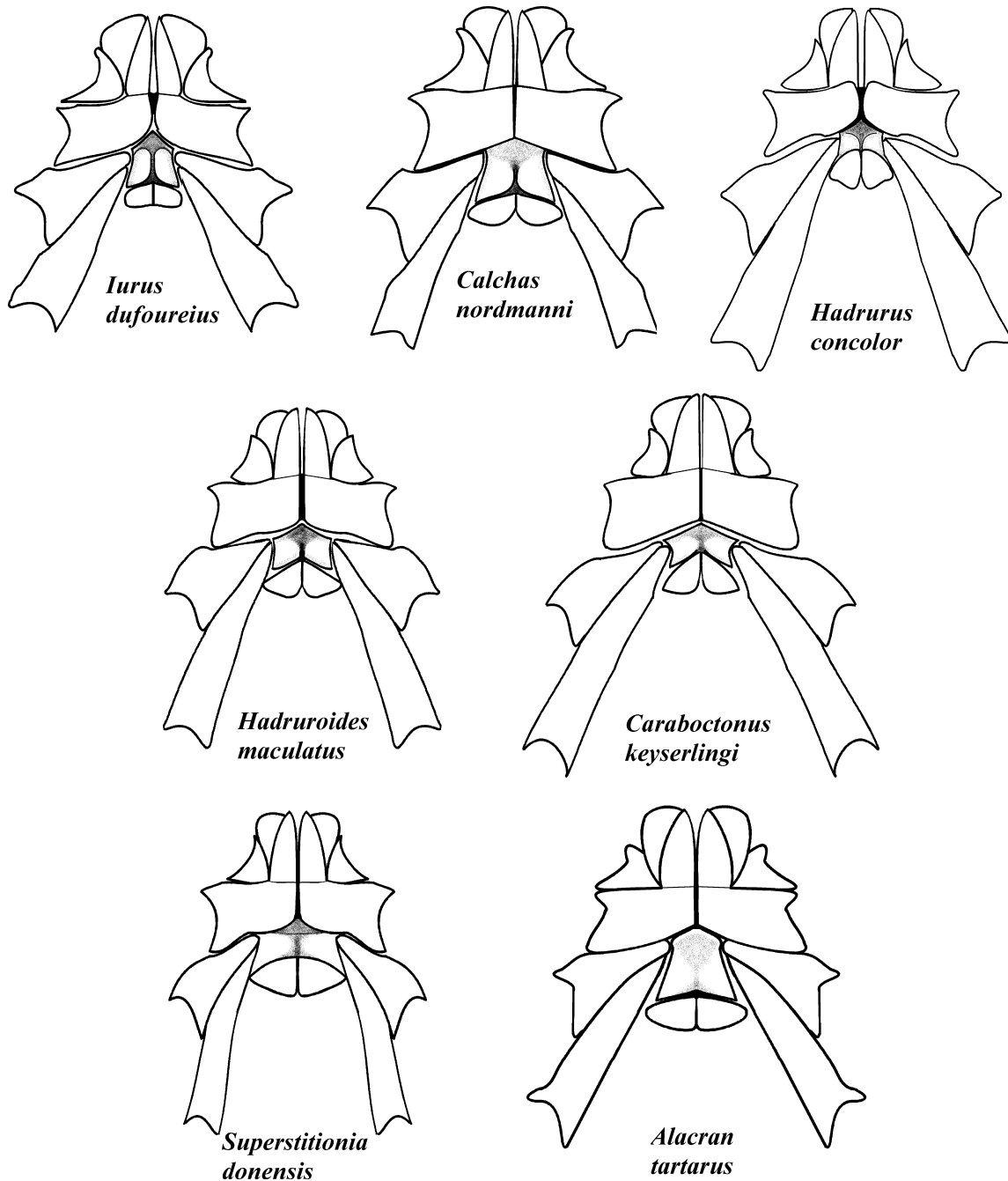
Figure 7: Sternocoxal area of Recent scorpion genera (*type 2* sterna), Vaejovidae.

Figure 8: Sternocoxal area of Recent scorpion genera (*type 2* sterna), Iuridae and Superstitioniidae.

quite elongated sternum but this must be attributed, in part, to its cave adaptation. This characteristic was used as one of many characters contrasting the scorpiopines with other subfamilies of Euscorpiidae by Soleglad & Sissom (2001: 108-109).

Apparent from Fig. 5, the ischnurids have an unique sternum that tapers slightly from an anterior to posterior direction, the most exaggerated in the genus *Liocheles*. This was also reported by Prendini (2000), and is dis-

cussed further in the section on morphometrics. This tapering tendency is also seen in *Hemiscorpius*, which forms a sister group to the ischnurids (Prendini, 2000: Fig. 2).

The sternum of the superstitioniids (Figs. 8, 9-13) is quite varied – from the much wider than long sternum of *Superstitionia* (Fig. 8, 9) which exhibits a distinct posterior emargination and apical depression to the species of *Typhlochactas* (Figs. 11, 13), *Sotanochactas* (Fig. 12),
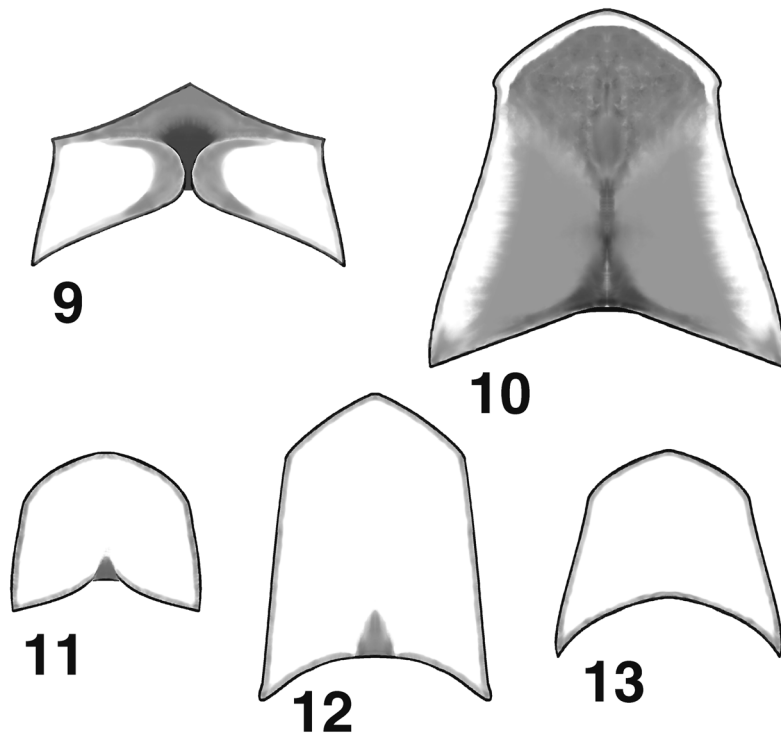
Figures 9-13: Sterna of Superstitioniidae. **9.** *Superstitionia donensis*. **10.** *Alacran tartarus*. **11.** *Typhlochactas mitchelli* (after Sissom, 1988, Fig. 3, in part). **12.** *Sotanochactas elliotti* (after Mitchell, 1971, Fig. 4, in part). **13.** *Typhlochactas granulosus* (after Sissom, et al, 1998, Fig. 2, in part). Note, posterior edges of sterna in Figs. 12 & 13 are not necessarily complete due to overlaying genital operculum in original figures.

and *Alacran* (Figs. 8, 10) that have equilateral to elongated sterna and very subtle posterior emarginations. Sissom (1988: 368) described this peculiar sternum "… anterior margin gently convex, posterior margin concave, lateral margins diverging distally; small posteriomedial depression present." In agreement with Sissom's description, common to both *Typhlochactas*, *Sotanochactas*, and *Alacran* (Figs. 8, 10-13), is the somewhat rounded apex, the subtle concave area emitting from the posterior emargination, and the lateral lobes that are *not* convex, all presumably a factor of cave adaptation, since the non-troglobitic member of its family, *Supersititionia* (Figs. 8, 9), has a typical *type 2* sternum.

Sternum types in fossil scorpions

We present a brief overview of fossil scorpion sterna described and/or illustrated in literature, in particularly those sterna that appear to be similar, at least in part, to the two sternal types described in this paper. Most of this information is from Kjellesvig-Waering (1986). Of particular interest are fossil scorpions assigned to infraorder Orthosterni, the primary scope of this paper.

Orthosterni (or Orthosternina of Kjellesvig-Waering (1986)): The sternum of the Carboniferous scorpion *Palaeopisthacanthus schucherti* Petrunkevitch has been discussed, described and/or illustrated by Petrunkevitch (1913: 48-49, pl. 2, Fig 8-9, Text-Figs. 11-12), Vogel & Durden (1966: Text-Fig. 2, 657), Kjellesvig-Waering (1986: Text-Figs. 103-104, 234) and Jeram (1994a: 524). Due to the poor condition of the

fossil in this particular area, the descriptions and illustrations do not agree in all aspects. Petrunkevitch (1913: 49) described the sternum: "… sternum is very large, distinctly pentagonal, with a recurved posterior edge …". Vogel & Durden (1966) illustrated a sternum whose anterior apex is rounded giving us a sternum that is slightly wider than long. In Kjellesvig-Waering's (1986) figures, the apex is pointed extending upward into leg coxae II, making the sternum slightly longer than wide. Both descriptions and illustrations do agree, however, as to the medial and posterior areas of the sternum, both noting a medial to posterior depression. Vogel & Durden (1966) state: "The interior of the sternum has a round anterior end, but is difficult to say what its shape would be on the outside. In the middle of the sternum is a mound, an inpouching of the body wall for muscle attachment." Kjellesvig-Waering (1986) states: "… the sternum is large and pentagonal. The anterior is not clear, but it definitely is triangular, giving a pentagonal shape to the sternum. In the center is an elliptical area that was sunk inward in life, undoubtedly for the attachment of muscles." Jeram (1994a) discusses both interpretations giving slight credence to Vogel & Durden's interpretation by stating "…Triangular area anterior to this which Kjellesvig-Waering (1986) interpreted as an anterior portion of the sternum may simply be due to the post-mortem separation of the second pair of coxae." Whether the entire area anterior of the visible region as illustrated by Vogel & Durden (1966) is the entire apex (as illustrated by Kjellesvig-Waering (1986)), or a portion of the apex, or, as Jeram (1994a) suggests, not a part of the sternum, we still have a five-

sided somewhat flat sclerite that exhibits a posterior depression. Therefore, we strongly suggest that the sternum of *Palaeopisthacanthus schucherti* conforms to *type 1* and consider it very similar to the simple flat sternum found in the Recent scorpion *Pseudochactas ovchinnikovi*. In this paper we have included the illustration provided by Kjellesvig-Waering (1986: Text-Fig. 104-B) for *Palaeopisthacanthus schucherti* (shown in our Fig. 3).

For other palaeopisthacanthids, Jeram (1994a: 538) reports the sternum of *Cryptoscorpius americanus* Jeram is subpentagonal with the length slightly exceeding its width, but does not mention any other structural details.

Kjellesvig-Waering (1986: 240) described the sternum of Upper Miocene scorpion *Mioscorpio zeuneri* (Hadži, 1931) as follows: "… sternum is small, deeply cleft at midsection, at least for the posterior three-fourths of the length … base seems to be straight … overall shape is pentagonal with parallel sides …". This description certainly is consistent with sternum *type 2* although it is not clear if the lateral lobes are convexed. Kjellesvig-Waering (1986) placed *Mioscorpio* into the modern family Scorpionidae, where it was listed also by Fet (2000).

Holosternina: Kjellesvig-Waering (1986) discussed and illustrated the following fossil sterna: In Text-Fig. 15, depicting Silurian scorpion *Stoermeroscorpio delicatus* Kjellesvig-Waering, we see an elongated pentagonal sternum with a median furrow which appears to be bifurcated. Kjellesvig-Waering (1986: 55) writes: "… large sternum is elongate-pentagonal with slightly tapering lateral margins … obtuse anterior … deep, inverted triangular basal margin …". Text-Fig. 26 shows an equilateral pentagonal sternum for *Gigantoscorpio willsi* Størmer with a posterior emargination outlining what appears to be lateral lobes (see our Fig. 3). Kjellesvig-Waering (1986: 76) states: "… sternum is very large, round, probably peaked at the anterior, giving it a rounded pentagonal shape. It has a deep median sulcus that seems to bifurcate in the middle …". In Text-Fig. 37-B, illustrating *Eoctonus miniatus* Petrunkevitch, we see a sternum very similar to the primitive form of *type 1*, as those exhibited in *Palaeopisthacanthus* and Recent scorpion *Pseudochactas*. It is essentially equilateral with a posterior depression. Kjellesvig-Waering (1986: 99) writes: "… sternum is very large, pentagonal in shape with an inverted rounded area at the posterior …". Text-Fig. 41-B depicts an elongated pentagonal sternum for species *Buthiscorpius lemayi* Kjellesvig-Waering showing a conspicuous posterior depression, again very similar to our *Type 1* sternum. Kjellesvig-Waering (1986: 103) comments: "… sternum is elongate-pentagonal, the base being incurved with the anterior triangular part hardly projecting forward. A deep sulcus … occurs in the posterior half of the plate …". Text-Fig.

43-B, C of species *Anthracoscorpio juvenis* Kušta, shows a flat pentagonal sternum. Kjellesvig-Waering (1986: 109) provides no additional information as to the detail of the sternum's surface. Kjellesvig-Waering (1986: 112), describing species *Coseleyscorpio lanceolatus* Kjellesvig-Waering, states "… Sternum: sides converging forward, base deeply notched … proportionately narrower, particularly anteriorly …". Kjellesvig-Waering (1986) placed these last four genera in his new superfamily Eoctonoidea.

Lobosternina: In Text-Fig. 97, Kjellesvig-Waering (1986) illustrates the sternum of *Pseudobuthiscorpius labiosus* Kjellesvig-Waering. This sternum is very interesting, the posterior appearing to be bifurcated but not exhibiting convex lateral lobes. Kjellesvig-Waering (1986: 219) writes: "… sternum is very large … overall pentagonal outline … deeply invaginated, roughly in a triangular depression in the posterior … narrow low ridge occurs transversely along the anterior part …".

Mesoscorpionina (classification of Stockwell's (1989)): Jeram (1994b: Fig. 4-G) illustrates a presumably *type 2* sternum for *Pulmonoscorpius kirktonensis*, definitely showing a posterior emargination. Its not clear, based on its description, however, whether this posterior emargination is accompanied with convexed lateral lobes. Jeram (1994b: 292-293) states: "… [in] juveniles the sternum is sub-pentagonal in shape, with a rounded anterior margin … posterior half there is a deep longitudinal median sulcus ..." "… only large specimen in which the sternum is well-preserved … sternum has been flattened and the posterior sulcus is represented by a longitudinal fold in the cuticle, which bifurcates anteriorly to form a Y-shaped crease …".

In summary, we see fossil sterna that apparently, in some respects, span both sternal types defined in this paper. These observations are based on external attributes only and in many cases the subtle three-dimensional aspects of the sternum surface are not known. Of particular importance is the establishment of *type 1* sterna for the palaeopisthacanthids, an important fossil group in the Orthosterni, the subject of this paper. Of the three genera placed in Palaeopisthacanthidae, we have information on the sternum for two, *Palaeopisthacanthus* (essentially complete data for one species) and *Cryptoscorpius* (partial data, shape only). Sternal *type 1* also appears in the infraorder Holosternina, in particular superfamily Eoctonoidea (identified for two genera). Under Stockwell's (1989) classification the eoctonoids essentially equate to his Palaeosterni, the sister group of Orthosterni, both under suborder Neoscorpionina. This interesting relationship as it pertains to the sternum is discussed further in the section on phylogenetic considerations.

Internal aspect of sternum

We studied the internal structure of the sternum for 46 genera spanning a major cross section of Recent scorpion groups (see Figs. 14-33 and 34-41). In general, the sternal plate internally is a mirror image of its external surface except the concave regions are convex and vice versa. However, protruding from the posterior medial area we find a conspicuous internal process(es) extending into the body cavity in an inward to posterior direction. These structures, to our knowledge, have not been previously described. The two sternum types defined in this paper are supported by this unique internal process(es): for sternum *type 1* a single simple rounded process is present (Figs. 14-19 and 34-37) and for sternum *type 2* the process is bilobed forming two processes (Figs. 20-33 and 38-41). We hypothesize that the internal process for *type 1* sterna is a direct derivation of the posterior depression found on the external surface, and the two internal processes found on *type 2* sterna are a derivation of the posterior emargination of the external aspect further emphasizing the bifurcation of the sternum posterior edge.

In addition to the internal processes, the edges of the apex and lateral edges of the sternum are folded somewhat and extend into the body cavity forming a squared edge on these surface extremities. The cuticle thins as the edge extends inward. When removing the sternum from the scorpion, this folded edge sometimes came off the plate altogether or irregularly disintegrated at its most inner aspects. Although this folded edge is shown in various forms in the illustrations depicting the internal aspect of the sternum, we do not consider it important in the analysis presented herein. Also of note is that the apex, especially for *type 1* sterna, is more rounded once removed, due, in part, to the overhang of the leg coxae II. When viewed externally while attached to the scorpion, the sternum apex forms a precise vertex caused by the rounded and symmetric inner aspects of leg coxae II and therefore this rounded apex (the apical "button") is partially hidden. The anterior aspect of the genital operculum often covers the extreme posterior edge of the sternum, especially in the buthoids thus covering the posterior outer ridge. By gently pushing the genital operculum plates downward slightly, the outer ridge becomes visible.

Type 1 sterna. The variability of the internal process exhibited in *type 1* sterna spans the spectrum from the very subtle convex projection as that found in *Pseudochactas* (Fig. 14) to the conspicuous elongated process of *Chaerilus* (Figs. 15, 34-35) that extends, internally, beyond the posterior edge of the sternum. The sternum cuticle of *Pseudochactas* is exceptionally thin, the internal projection is minimal, only reflecting the convex counterpart of the shallow posterior depression,

showing no extra development. Its very flat structure visible externally is also the case internally, providing no three-dimensional aspects except for the subtle internal process. For *Chaerilus*, the sternum exhibits a subtle but well defined three-dimensional quality showing a slight apical "button" (Fig. 35). In all cases, however, the internal process of *type 1* sterna is a single rounded projection that emanates from the posterior depression, its base, externally or internally, never bisecting the posterior ridge. In Figs. 34-37 we illustrate in detail the posterior and lateral views of the sternum for genera *Chaerilus* and *Tityus*. In these illustrations we can see that the internal projection is at its largest posteriorly and reduces in size as it extends anteriorly along the median furrow of the sternum, terminating at the beginning of the apex. In the sternum of *Tityus* we can see the highly convex structure of the sternum exhibiting a deep concave region terminating into the small apical "button". Based on the limited material dissected, it appears that Old World buthids (Figs. 16-17) have their internal process more reduced, not extending internally beyond the posterior edge nor extending anteriorly towards the apex, whereas in New World buthids (Figs. 18-19 and 36-37), the internal process is vertically longer, extending slightly beyond the posterior edge as well as further anteriorly thus implying more development.

Type 2 sterna. The internal posterior processes, one per lateral lobe, originate at the inner anterior edges of the lateral lobes, emanating into the body cavity in a slightly posterior direction: the internal processes begin at the top of the inner aspect of the lateral lobes and extend down the inner edge to the emargination in the posterior edge of the sternum. The processes are the most defined and extend the furthest into the body cavity at the posterior portion where their distal aspects flare outwards toward the lateral edges of the sternum. The degree of development of these processes, however, vary considerably depending on the scorpion group: highly developed in the iurids, especially in genera *Hadrurus* (Figs. 21, 38-39) and *Hadruroides* where the length of the internal processes approach the length of the sternum itself; weakly developed in the ischnurids (Fig. 24), where processes are only pigmented ridges outlining the inner edges of the lateral lobes. In *Liocheles* (Fig. 5), whose sternum is quite flat and the lateral lobes very subtle, the ridges are limited to small pigmented posterior granules. In some cases, for those processes that are arranged in close proximity, they are partially connected by cartilage, minimizing their bilobed appearance (e.g., *Anuroctonus*). For small species, the extremities of these processes may deteriorate into cartilage, not showing a distinct well delineated form (e.g., *Superstitionia*, some small bothriurids). Two highly different extremes of internal process development are illustrated in scorpion genera *Hadrurus* (Figs. 38-39) and *Bothriurus* (Figs. 40-41). In the former, the processes are quite elongated
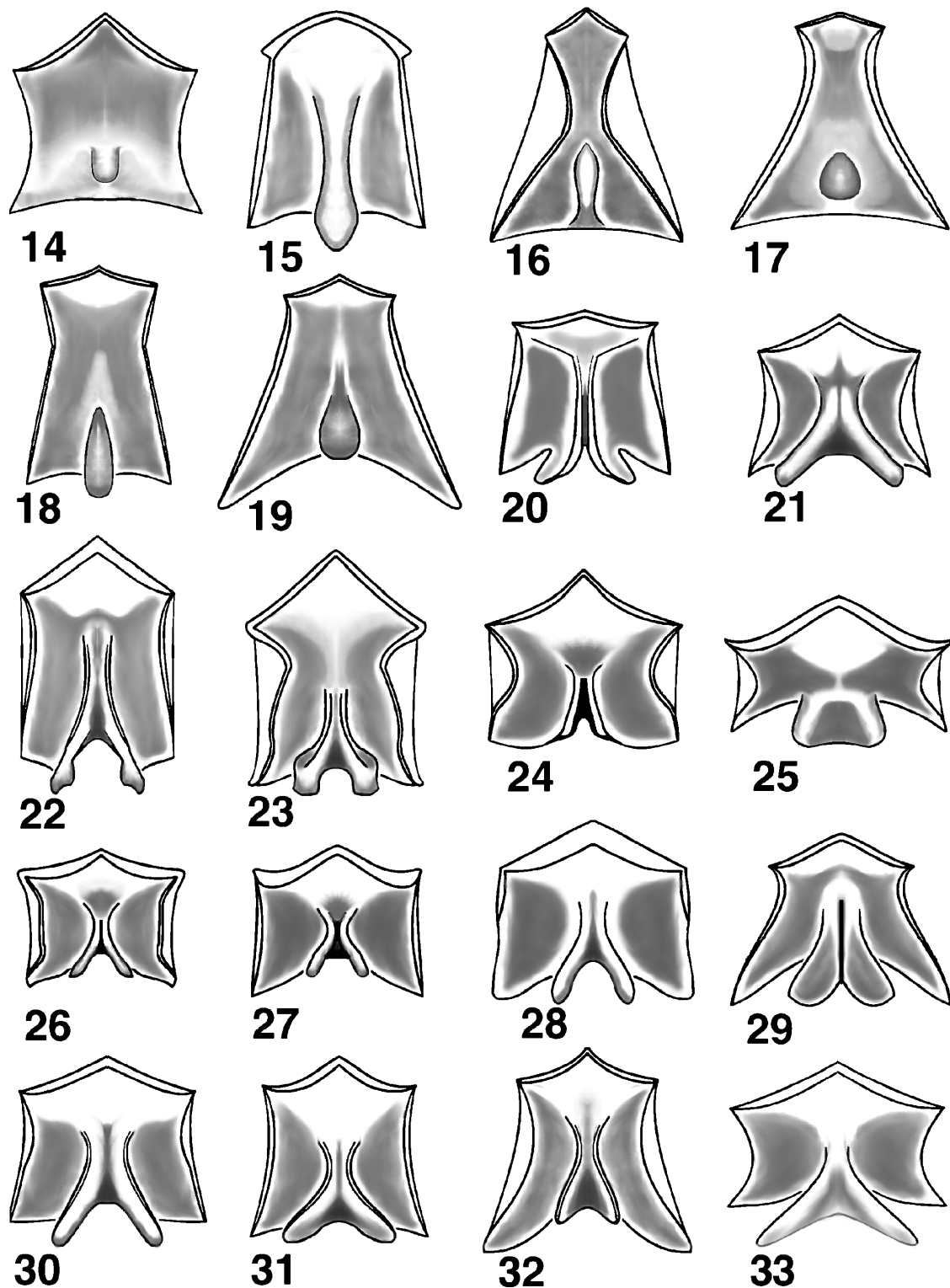
Figures 14-33: Internal view of scorpion sternum showing posterior process(es) for sternum *types 1* (Figs. 14-19) and *2* (Figs. 20-33). Note, sternum is angled vertically in order to show profile of posterior process(es), therefore proportions are skewed (*apex* is closest to the horizontal plane). **14.** *Pseudochactas ovchinnikovi* **15.** *Chaerilus variegatus* **16.** *Apistobuthus pterygocercus* **17.** *Mesobuthus caucasicus* **18.** *Centruroides exilicauda* **19.** *Rhopalurus junceus* **20.** *Iurus dufoureius* **21.** *Hadrurus concolor* **22.** *Heterometrus longimanus* **23.** *Diplocentrus ochoterenai* **24.** *Opisthacanthus lepturus* **25.** *Brachistosternus* sp. **26.** *Megacormus gertschi* **27.** *Euscorpius italicus* **28.** *Chactas* sp. **29.** *Brotheas granulatus* **30.** *Vaejovis punctipalpi* **31.** *Serradigitus subtilimanus* **32.** *Smeringurus mesaensis* **33.** *Superstitionia donensis*.
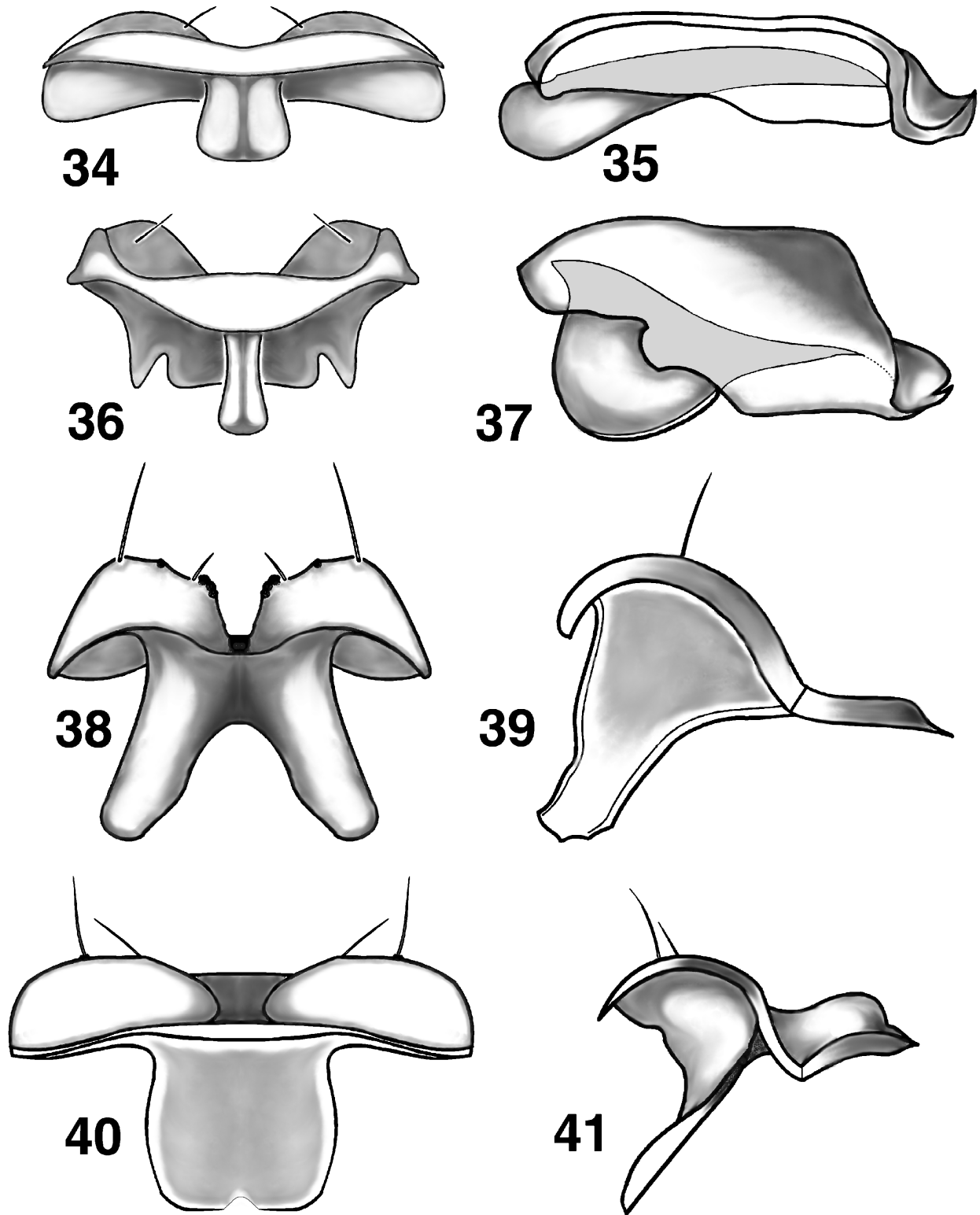
Figures 34-41: Posterior and lateral view of scorpion sternum *types 1* (Figs. 34-37) and *2* (Figs. 38-41) showing internal process(es). **34-35.** *Chaerilus variegatus* **36-37.** *Tityus nematochirus* **38-39.** *Hadrurus concolor* **40-41.** *Bothriurus burmeisteri.* Shaded area in Figs. 35 and 37 show the hidden upper extension of the internal process where it connects to the median furrow; connecting line depicts the median furrow as it extends most of the length of the sternum.

forming a conspicuous fork when viewed from a direct posterior direction (Fig. 38) and also extend anteriorly as they outline the inner edges of the lateral lobes up to the apex (Fig. 39). In *Bothriurus*, the internal processes are partially coalesced (Fig. 40) and highly flattened (Fig. 41) by a hypothesized vertical compression of the sternum. The medial area of this flattened internal process pair is quite thin, sometimes semi-transparent, where it thickens at the extreme lateral edges, presumably the original internal processes. The subtle pigmentation supports this observation (also see Fig. 25 illustrating *Brachistosternus*). This configuration as illustrated for *Bothriurus* is found also in other bothriurid genera studied for this paper. For smaller bothriurid species, the flattened coalesced internal processes are very delicate, the medial transparent area more cartilage-like than chitinous, not forming a discrete edge. The separation of the lateral lobes in the bothriurids was noted by Stockwell (1989: 87), in his discussion of the bothriurid sternum, where he writes "It is not, as popularly described, reduced to a pair of narrow, transverse sclerites [our lateral lobes] (Lamoral, 1980), although the median longitudinal furrow that is present on all scorpion sterna, and almost completely bisects the short sternum of bothriurids, may contribute to such an interpretation." Of course, we take exception to Stockwell's statement that the "median longitudinal furrow […] is present on *all scorpion* sterna", since we have demonstrated that it is certainly absent in *type 1* sterna. We strongly suggest here that the bifurcation of the posterior edge proposed for *type 2* sterna, which distinguishes it from *type 1* sterna, is validated by the bilobed internal process: clearly, as evidenced in Figs. 20-33, the splitting of this process is visible for most of the inner aspects of the lateral lobes.

Sternum compression within types

As discussed elsewhere in this paper, Petrunkevitch (1953) established that the bothriurid sternum, once "flattened", was "pentagonal". This vertical "folding" of the bothriurid sternum is quite evident in Fig. 41, exhibiting a radical bending of the sternum at the lateral lobe/apex juncture. We suggest here that the buthoid sternum would also show a typical "pentagonal" shape if it was flattened out. We present an argument here suggesting that the unusual sternum variants as found in the buthoids, *type 1*, and the bothriurids, *type 2*, can be explained by hypothesizing a series of degrees of incremental compression. By analyzing these degrees of compression we can hypothesize intermediate forms of this derivation, from a basic sternum shape to one that is highly compressed. We argue here that these two sterna variants do not exhibit fundamental sternum differences, as for example, the two sternal types established in this paper, but instead are just a modification of the sternum due to compression. Also, starting from a presumed

basic sternum within a type, we can, in general, determine the direction of this compression. For example, for *type 1* sterna, the narrower and anteriorly tapered sternum found in typical buthoids can be formed, in part, by compression from an anterohorizontal direction on both lateral sides of a "regular" sternum. Similarly, the significantly wider than long sternum found in the bothriurids with the flattened apex and separated lateral lobes can be formed by compression from a vertical direction, which we propose here is from the leg coxae II since the apex is considerably flattened. We use the term "compression" because this is the observed effect on a, otherwise, normally constructed sternum within its sternal type. The directions of compression used in this paper, vertical and horizontal, are from the frontal plane perspective of the sterna external views illustrated in Figs. 42-43. Of course, we offer no reason for the compression, as we offer no reason for most of the derivations that occur in scorpions.

Horizontal compression – the buthoids. We hypothesize here that horizontal compression, in particular at the anterior half of the sternum, is a probable cause of the narrowing in many typical buthid sterna. The sternum of *Pseudochactas* (Fig. 3 and 14), which is essentially flat with subequal length sides, shows no compression whatsoever. Its posterior depression is minimal, the outer ridge only evident posterior of this depression, no evidence of a median furrow, the internal process is quite subtle, and in all, the sternum showing little concavity or convexity on its external and internal surfaces. Consequently, we strongly suggest here that the *Pseudochactas* sternum is the most primitive of any Recent scorpion, showing a close affinity with the sternum illustrated by Kjellesvig-Waering (1986) for the Carboniferous scorpion *Palaeopisthacanthus* (shown in our Fig. 3). They both appear flat with sub-parallel lateral sides and exhibit a limited posterior depression. The *Chaerilus* sternum shows minimal compression anteriorly, which is reflected by the subtle wide concave region that tapers into the deep posterior depression (Fig. 3). The corresponding internal process is well developed, however (Figs. 15, 34-35), as one would expect with the deep posterior depression.

We suggest here that anterior horizontal compression present in most buthid sterna is the probable cause for the exaggerated "triangular" description so commonly attached to the buthid sternum, although in Figs. 3-4 we see the complete spectrum from highly compressed to slightly compressed as exhibited by such genera as *Karasbergia* or *Microtityus*. Figure 42 illustrates the hypothesized effects of horizontal-anterior compression of *type 1* sterna. In this figure we begin with a *Pseudochactas*-like sternum showing gradual degrees of compression until we reach a typical buthid sternum. One could argue that the intermediate stages shown in Fig. 42 are representative of those present in chaerilids

Soleglad & Fet: Scorpion Sternum
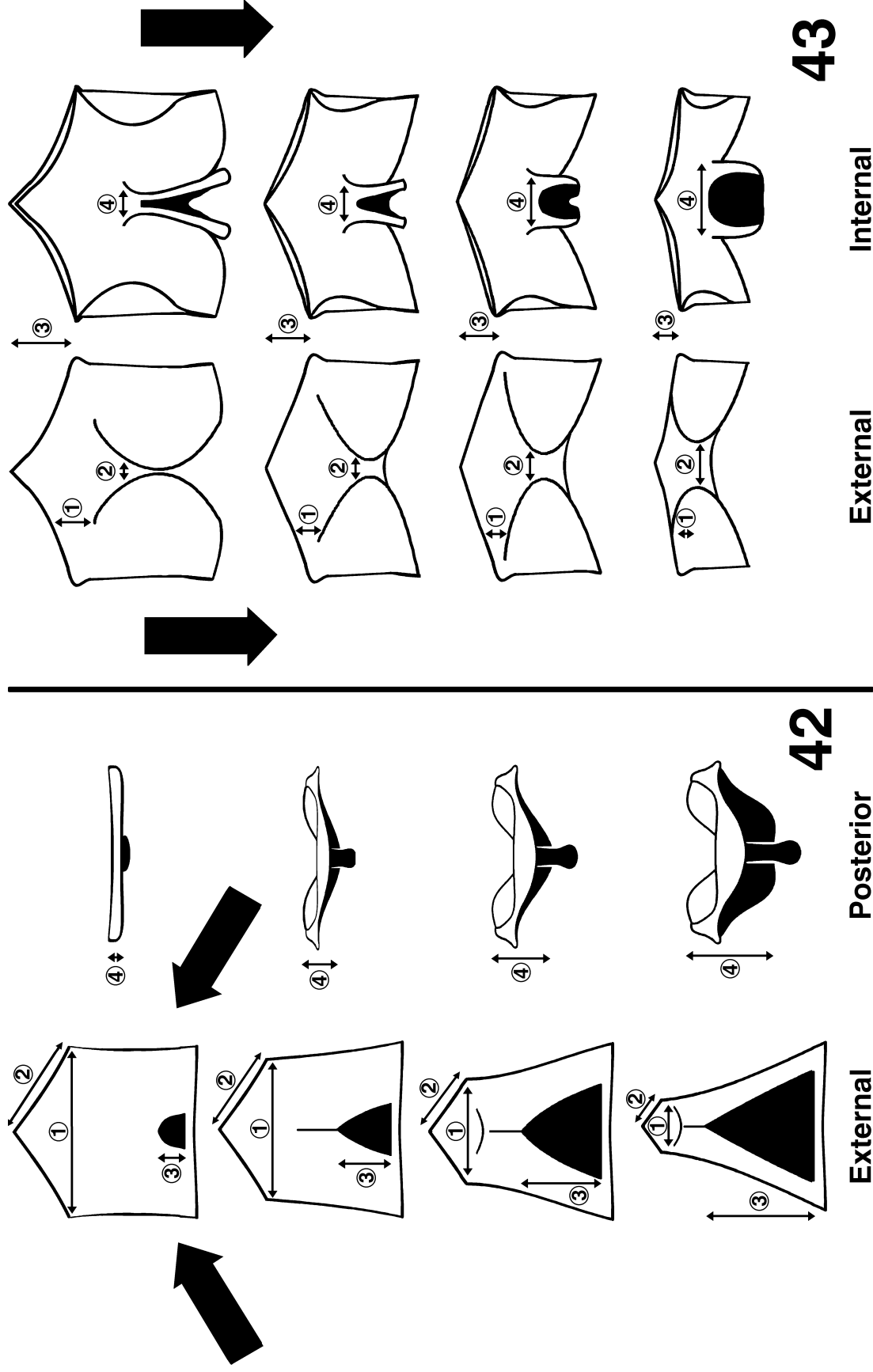
Figures 42–43: Diagrammatic view of external, posterior and internal aspects of scorpion sternum depicting hypothesized incremental affects of *horizontal* and *vertical compression* of the sternum as exhibited in families Buthidae (*type 1* sternum) and Bothriuridae (*type 2* sternum). **42.** *Horizontal compression* in buthids: 1 = compression forcing narrowing of anterior aspect of sternum at the apex base; 2 = compression forcing shortening of apex lateral edges; 3 = compression forcing the inward folding of the sternum, resulting in a deeper, wider and longer posterior depression, the sternum becoming quite concave; 4 = same as 3 but showing expansion of internal process and bottom aspect of posterior depression. Also note in latter stages of compression the apex buckles slightly forming a small convex tip of the sternum. **43.** *Vertical compression* in bothriurids: 1 = compression of sternum apex forcing abutment of anterior aspect of lateral lobes with leg coxae II; 2 = compression forcing conspicuous separation of inner aspect of lateral lobes; 3 = compression forcing a flattening of the apex; 4 = compression forcing the widening, flattening and partial coalescing of the internal processes. Heavy arrows indicate direction of compression: for the buthids it is in a horizontal-anterior direction; for the bothriurids it is in a vertical-posterior direction.

and buthoids with minimal narrowing of the anterior aspect of the sternum. We see that as the compression becomes more defined, the sternum folds somewhat inwardly creating the concave region which encompasses a large portion of the medial to posterior aspects of the sternum. Consequently, the posterior depression becomes deeper, wider and longer, as evidenced by the well developed internal process. These effects, in part, are caused by the shortening of the apex lateral edges and the narrowing of the apex width. In addition, the compression causes the apex to buckle upward forming a small convex "button-like" tip (visible when the sternum is removed). The sternum of *Tityus* illustrated in Figs. 36-37 is an excellent example of a highly compressed sternum, the posterior view in particular shows the inward folding of the sternum creating a significant concave region. In the "typical" buthid sternum we see the outer ridge is present laterally for most of the middle to posterior aspects of the sternum, again caused by the wide spread convex region. For sterna showing less or no compression the ridge is isolated more to the medial posterior edge delineating the posterior depression, as evidenced in *Pseudochactas* and, in part, *Chaerilus*.

Vertical compression – the bothriurids. We suggest here that the very short and wide sternum exhibited in the family Bothriuridae is probably caused by vertical compression of the sternum, primarily from the direction of leg coxae II. In Figure 43 we show the hypothesized effects of vertical compression on the bothriurid sternum as increments in development for both the external and internal aspects. As was the case with *type 1* compression discussed above, the intermediate stages of sternum compression may be representative of bothriurids that exhibit minimal compression (this issue is discussed further in the section on **Phylogenetic and Taxonomic Considerations**). The unique vertical compression of the bothriurid sternum can be quantified with four derivations as illustrated in Figure 43: (1 & 3) as the sternum is compressed vertically from a leg coxae II to posterior direction, we see the apex being flattened considerably (3), and the anterior edges of the lateral lobes abutting with leg coxae II (1); (2) as the sternum apex is flattened, the lateral lobes are pushed outward creating a conspicuous gap between their inner edges; and (4) internally, the flattening of the apex and the widening of the gap between the lateral lobes forces a widening at the base of the internal processes which flattens and partially coalesces the two internal processes. The external extremities of the two processes are slightly visible in figures illustrating *Brachistosternus* (Fig. 25) and *Bothriurus* (Fig. 40). The mechanism of this flattening can be further explained by comparing the lateral aspects of the sterna of *Hadrurus* and *Bothriurus* shown in Figs. 39 and 41: In *Hadrurus*, an iurid, the basal anterior edge of the internal process (i.e., the right side in the figure) is extended to the base of the apex, the top of the lateral

lobes. In *Bothriurus*, the flattened apex has pushed the basal anterior edge of the processes posteriorly, thus flattening them. This unique form of the bothriurid internal processes has been verified in seven out of 12 known genera.

Morphometrics

We constructed five morphometric ratios based on measurements of the sternum and leg coxae II-IV (see Fig. 1 and **Methods & Material** section for method of measurement). The choice of these ratios is somewhat intuitive, based on the hypothesized compression of the sternum discussed in detail above. Hopefully, these ratios should further quantify, to a degree, this compression. For example, the *vertical compression* exhibited in the bothriurids resulting in a wider and shorter sternum (i.e., "transverse") can be further quantified by comparing the sternum's length and posterior width as well as comparing the relative proportions of the apex lateral side. Likewise, the *anterior horizontal compression* as seen in most buthids resulting in the extreme narrowing of the distal aspect of the sternum (i.e., "triangular") can be further examined by comparing relative proportions of the apex lateral edge as well as comparing the anterior and posterior sternum widths which are indicative of a "tapering effect". Another possible effect of a narrowing sternum is the elongation of leg coxae III and IV which abut its lateral sides. The elongation is caused, in part, since the inner aspects of the coxae must extend further inward to meet the narrowed sternum.

The five ratios are: 1) *coxa II length/sternum apex side length*: this ratio illustrates a narrowing of the anterior aspect of the sternum as well as a widening of the sternum thus is indicative of both horizontal and vertical compression; 2) *sternum posterior width/sternum apex width*: this ratio demonstrates a tapering of the sternum anteriorly, an indicator of horizontal compression; 3) *coxa III length/coxa II length*: this ratio measures the degree of elongation in leg coxa III, a possible indicator of the narrowing of a sternum; 4) *coxa IV length/coxa II length*: this ratio measures the degree of elongation in leg coxa IV, a possible indicator of the narrowing of a sternum; 5) *sternum length/sternum posterior width*: this ratio measures the overall length/width proportions of the sternum, which can indicate possible vertical compression. Note that we use leg coxa II in the ratios since it appears relatively uniform in proportions across scorpions in general, thus providing a constant when emphasizing the relative differences in the other morphometrics where variability is expected.

The results of these morphometric ratio comparisons are shown in Tables 1 and 2: Table 1 measures differences in families and subfamilies across the order and

	$\dfrac{\text{Coxa II}_L}{\text{Sternum}_{AL}}$	$\dfrac{\text{Sternum}_{PW}}{\text{Sternum}_{AW}}$	$\dfrac{\text{Coxa III}_L}{\text{Coxa II}_L}$	$\dfrac{\text{Coxa IV}_L}{\text{Coxa II}_L}$	$\dfrac{\text{Sternum}_L}{\text{Sternum}_{PW}}$
Palaeopisthacanthidae (1)	1.41 (1.407)	0.94 (0.944)	0.95 (0.947)	1.32 (1.316)	1.32 (1.324)
Pseudochactidae (1)	**2.11 (2.111)s**	**1.19 (1.194)s**	**1.05 (1.053)s**	**1.58 (1.579)s**	**1.08 (1.081)s**
Chaerilidae (3)	2.44-2.80 (2.666)	1.11-1.36 (1.245)	1.08-1.24 (1.154)	1.62-1.76 (1.673)	1.03-1.23 (1.115)
Buthidae[1] (30)	**3.60-13.00 (7.468)l**	**1.08-3.50 (2.008)l**	**1.30-1.67 (1.515)l**	**2.11-2.86 (2.481)l**	0.67-1.66 (1.163)l
Iuridae (6)	2.41-3.62 (3.168)	0.87-1.36 (1.125)	1.17-1.35 (1.276)	1.76-2.61 (2.252)	0.67-1.04 (0.816)
Iurinae (2)	**3.29-3.33 (3.310)l**	**1.28-1.36 (1.319)l**	1.17-1.27 (1.224)	1.76-1.95 (1.855)	0.82-1.04 (0.934)
Caraboctoninae (4)	2.41-3.62 (3.097)	0.87-1.12 (1.029)	**1.25-1.35 (1.302)l**	**2.33-2.61 (2.450)l**	0.67-0.83 (0.758)
Bothriuridae (7)	**1.79-2.30 (2.069)s**	0.95-1.05 (1.017)	0.93-1.24 (1.109)	1.78-2.43 (2.113)	**0.42-0.54(0.487)s**
Scorpionidae (5)	3.05-3.42 (3.243)	1.00-1.08 (1.039)	1.09-1.19 (1.148)	1.16-1.75 (1.544)	0.93-1.69 (1.175)
Diplocentridae (6)	1.60-2.95 (2.240)	1.19-1.19 (1.194)	1.05-1.31 (1.163)	1.55-1.74 (1.654)	0.89-1.38 (1.188)
Urodacidae (1)	2.47 (2.471)	1.19 (1.192)	**0.98 (0.976)s**	1.81 (1.810)	0.87 (0.871)
Ischnuridae (5)	1.85-2.47 (2.288)	**0.74-0.97 (0.860)s**	0.96-1.09 (1.029)	**1.06-1.66 (1.426)s**	1.03-1.25 (1.141)
Hemiscorpiidae (2)	2.58-2.78 (2.681)	0.86-0.92 (0.889)	1.00-1.10 (1.048)	1.81-1.85 (1.828)	**1.35-1.44 (1.396)l**
Euscorpiidae (9)	2.37-3.58 (2.984)	1.02-1.48 (1.181)	1.06-1.23 (1.137)	1.53-1.93 (1.731)	0.61-1.58 (1.051)
Euscorpiinae + Megacorminae (4)	2.37-3.14 (2.778)	1.06-1.48 (1.245)	1.12-1.23 (1.157)	1.76-1.93 (1.809)	0.61-1.05 (0.803)
Scorpiopinae (5)	2.57-3.58 (3.148)	1.02-1.26 (1.129)	1.06-1.17 (1.121)	1.53-1.77 (1.668)	1.05-1.58 (1.249)
Chactidae[2] (9)	2.17-3.64 (2.699)	1.04-1.58 (1.191)	1.00-1.26 (1.129)	1.30-1.95 (1.735)	0.62-1.07 (0.900)
Vaejovidae (13)	2.35-4.09 (3.244)	1.16-1.62 (1.303)	1.13-1.32 (1.219)	1.65-2.32 (1.990)	0.60-0.94 (0.784)
Superstitioniidae (2)	2.33-3.46 (2.897)	1.21-1.37 (1.287)	1.10-1.17 (1.131)	1.94-1.95 (1.948)	0.59-1.00 (0.793)

Table 1: Sternocoxal morphometric ratio statistics broken down into scorpion families and/or subfamilies: Value following taxon is the number of samples per calculation, generally specifying number of genera, though in some cases multiple species are included. For Recent scorpions, largest and smallest mean values are specified for sterna *types 1* (first four rows: note, *Palaeopisthacanthus* is not included in the mean value comparisons) and *2* (remaining rows): **l** = *largest* mean value: **s** = *smallest* mean value. For sternum *type 1*, the first four ratios are indicative of *horizontal* compression of the sternum, the taxa with the largest mean value, the buthids, shows the most compression (shown in rectangle). For sternum *type 2*, ratios Coxa II$_L$/Sternum$_{AL}$ and Sternum$_L$/Sternum$_{PW}$ are indicative of *vertical* compression of the sternum, the taxa with the smallest mean value, the bothriurids, shows the most compression (shown in rectangle). Data for *Palaeopisthacanthus* is based on Kjellesvig-Waering's (1986) interpretation and illustration of sternum of *P. schucherti*. $_{AL}$ = apex lateral side length; $_{AW}$ = apex horizontal width; $_{PW}$ = posterior width; $_L$ = length. [1] Includes *Microcharmus* (Microcharmidae); [2] Includes two genera with unclear placement: *Anuroctonus* (now in Iuridae) and *Belisarius* (now in Troglotayosicidae).

Table 2 shows a detailed breakdown of statistics for the several buthoid genera examined in this study. It must be stressed here that this data is presented only to indicate a general trend in the support of the hypothesized compression discussed in this paper. Many of the measurements are based on a single specimen from one species in a genus (though in some cases, multiple species were included, e.g., *Chaerilus*, *Vaejovis*, *Diplocentrus*). Although one would not expect excessive variability in the proportions of these basic sternocoxal plates, the statistics presented here are still based on minimal sampling. The ratios for *Palaeopisthacanthus* were derived directly from the original Kjellesvig-Waering's figure (1986: Text-Fig. 104-B) shown in our Fig. 3.

Families/subfamilies: Horizontally, Table 1 is divided into two areas: the first four rows address *type 1* sterna and the remaining rows consider *type 2* sterna. Vertically, the first four ratios represent morphometric ratios that reflect horizontal compression and ratios one and five (i.e., in columns one and five) are indicators of vertical compression. For both sterna types we indicate the largest and smallest mean value for each ratio. Largest or smallest ratio mean values that are considered indicators of horizontal or vertical compression are enclosed in *rectangles*.

Type 1 **sterna.** It is interesting to note that the four taxa groups representing *type 1* sterna show a consistency across all four morphometric ratios with the palaeopisthacanthids showing the least horizontal compres-

	$\dfrac{\text{Coxa II}_L}{\text{Sternum}_{AL}}$	$\dfrac{\text{Sternum}_{PW}}{\text{Sternum}_{AW}}$		$\dfrac{\text{Coxa III}_L}{\text{Coxa II}_L}$	$\dfrac{\text{Coxa IV}_L}{\text{Coxa II}_L}$
*Microcharmus**	4.394	1.075	*Karasbergia**	1.333	2.111
*Karasbergia**	3.600	1.278	*Microtityus**	1.378	2.189
*Microtityus**	4.933	1.231	*Razianus*	1.432	2.108
Tityus	5.733	1.304	*Uroplectus**	1.300	2.350
*Uroplectus**	5.000	1.714	*Grosphus*	1.387	2.226
*Parabuthus**	6.094	1.800	*Alayotityus**	1.432	2.270
Liobuthus	6.600	1.556	*Microcharmus**	1.414	2.379
*Alayotityus**	6.167	1.833	*Parabuthus**	1.462	2.308
*Rhopalurus**	5.143	1.900	*Rhopalurus**	1.444	2.361
Orthochirus	8.200	1.417	*Hottentotta*	1.467	2.400
*Mesobuthus**	7.167	1.800	*Odontobuthus**	1.500	2.433
Kraepelinia	8.000	1.692	*Compsobuthus**	1.447	2.526
*Lychas**	6.667	2.361	*Polisius*	1.576	2.447
Grosphus	5.741	2.333	*Mesobuthus**	1.535	2.535
*Centruroides**	6.333	2.105	*Centruroides**	1.526	2.579
Anomalobuthus	7.600	1.842	*Babycurus*	1.567	2.500
*Compsobuthus**	6.333	2.333	*Isometrus*	1.562	2.531
*Odontobuthus**	8.000	1.850	*Vachoniolus**	1.525	2.500
*Vachoniolus**	8.889	1.846	*Lychas**	1.528	2.611
Buthacus	8.286	2.000	*Androctonus*	1.556	2.556
*Microbuthus**	7.000	2.500	*Liobuthus*	1.606	2.455
Isometrus	7.619	2.333	*Kraepelinia*	1.667	2.500
*Apistobuthus**	8.333	2.059	*Tityus*	1.535	2.651
*Paraorthochirus**	11.333	1.833	*Apistobuthus**	1.600	2.540
Androctonus	9.000	2.273	*Orthochirus*	1.585	2.585
Hottentotta	9.000	2.500	*Leiurus**	1.590	2.615
Babycurus	10.000	2.556	*Anomalobuthus*	1.579	2.842
Polisius	10.625	2.500	*Paraorthochirus**	1.588	2.735
Razianus	9.250	3.500	*Buthacus*	1.655	2.724
*Leiurus**	13.000	2.900	*Microbuthus**	1.667	2.857

Table 2: Sternocoxal morphometric ratio statistics broken down for buthoid genera as follows: genus order is based on the cumulative rank of least horizontal compression across two sets of ratios, the narrowing of sternum apex and the elongation of leg coxae III and IV. For example, *Microcharmus* reflects the least compression with a cumulative rank of three (i.e., it ranked second and first for the two first ratios) while *Leiurus*, with a cumulative rank of 59 (ranking last and next to last), exhibits the most compression. Similarly, *Karasbergia* reflected the least elongation of the leg coxae and *Microbuthus* showed the most elongation. Combining cumulative ranks across both ratio sets, *Karasbergia* and *Microtityus* overall reflect the least horizontal compression based on minimal narrowing of the sternum apex and minimal elongation of the leg coxae and *Leiurus* and *Microbuthus* exhibited the most overall horizontal compression. * indicates genera that are consistently within top, middle, and bottom ten rankings for all four ratios. $_{AL}$ = apex lateral side length; $_{AW}$ = apex horizontal width; $_{PW}$ = posterior width; $_L$ = length.

sion (i.e., a smaller mean value) and the buthids exhibiting the most compression (i.e., the largest mean value). However, this result is expected. For Recent scorpions, *Pseudochactas* has the least compression for this sternum type. The mean value differences between the buthids and chaerilids is considerable for these four ratios, spanning 31-180%. What is also interesting is that the buthids reflect considerable variability in the two ratios indicating a tapering of the sternum, exhibiting large coefficients of variability over 26%. Although the means show consideration separation from the other groups, the minimum buthid value of each ratio range is quite close to the next closest taxon. This is to be expected, however, as we see there are many buthids that do not reflect

much horizontal compression (i.e., *Karasbergia*, *Micro-charmus*, *Microtityus*, etc.). For the second set of ratios, those indicating elongation of leg coxae III and IV, we see much less variability in the buthids, the data ranges much smaller, reflecting a modest 6-8% in their coefficient of variability. This implies that the buthid leg coxae III and IV are elongated in general, regardless of whether the sternum shows anterior tapering. See discussion below on the buthids for more data on this issue.

Type 2 **sterna.** The large assemblage of scorpion groups comprising *type 2* sterna reflects a small range of mean values for ratio Coxa II$_L$/Sternum$_{AL}$ ranging from 2.069 to 3.310. The smallest mean value is that of the bothriurids indicating that the sternum apex lateral side is relatively large, definitely implying a widening of the sternum. In support of this ratio, the ratio Sternum$_L$/Sternum$_{PW}$ also reflects a wide sternum for the bothriruids which also has the smallest mean value for this sternum type. It is interesting to see that *Caraboctonus* and *Superstitionia*, both with somewhat wide sterna, do not exhibit the attributes of compression as that described for the bothriurids, their lateral lobes are not separated internally nor do the anterior edges abut with leg coxae II. Therefore, it is clear that one cannot use ratios alone to typify the bothriurid sternum. Ratio Sternum$_{PW}$/Sternum$_{AW}$ is the smallest for the ischnurids which indicates an unusual tapering from an anterior to posterior direction (notice that the posterior width is always smaller than the apex width in all four samples). This characteristic, in part, was reported by Prendini (2000: 48) for genera *Iomachus* and *Liocheles*, although he tied it in with an "equilateral pentagon" which is not considered here. *Hemiscorpius* also reflects this same divergence of the anterior sternum aspect. It is interesting to point out that the New World iurids (i.e., subfamily Caraboctoninae) have elongated leg coxae III and IV, especially coxa IV, *Hadrurus* showing the largest ratios of the three genera. Considering the ratio that compares gross sternum proportions, Sternum$_L$/Sternum$_{PW}$, *Hemiscorpius* has the largest ratio, with subfamily Scorpiopinae exhibiting the second largest ratio mean value. Note that the troglobitic genus *Troglocormus* has the most elongated sternum (ratio value = 1.583), consistent with the scorpiopines in general, but much of this attenuation is undoubtedly due to cave adaptation.

Comparisons across sternum types: For ratios depicting tapering of the sternum anteriorly, clearly the buthids exhibit the largest mean values across both sternum types, with the Old World iurids (subfamily Iurinae) showing the largest value for *type 2* sternum scorpions. Mean value differences between these two scorpions groups are considerable, 126% and 52% for ratios Coxa II$_L$/Sternum$_{AL}$ and Sternum$_{PW}$/Sternum$_{AW}$, respectively. Ratios indicating leg coxae elongation are also interesting: For leg coxa III, the buthids exhibit a modest

mean value difference (15.6%) over the New World iurids, and for leg coxa IV, they are essentially the same.

Buthidae/Microcharmidae: Table 2 details morphometric ratio data for 30 buthoid genera and is divided vertically and horizontally into two areas: vertically, the first two morphometric ratios are indicators of a narrowing sternum due to horizontal compression and the second two ratios reflect degrees of elongation of leg coxae III and IV, which may or may not reflect this compression. The buthid and microcharmid genera are ordered for these two ratios sets based on their degrees of compression and elongation exhibited: the genera with the less compression or elongation are listed first, the genera with the most compression or elongation are listed last. Horizontally, Table 2 is divided into gross sections of compression indicators, the upper section, delineating the least compression and coxae elongation, shows ten rows of which seven genera are found in all four ratio comparisons. Similarly, the bottom ten rows, indicating significant compression and coxal elongation, four genera are found in all four ratio comparisons. We consider these genera the best representatives of compression and elongation, or the lack of same. The middle section includes those genera that definitely show compression but not to exaggerated degrees. Per ratio set, the genera are assigned weights based on their overall position in ratio comparisons (i.e., first to last). These weights are totaled per ratio set, thus their final rank. *Microcharmus* indicates the least anterior tapering of the sternum whereas *Karasbergia* exhibits the least elongation of leg coxae III and IV. *Microtityus* and *Uroplectus* are consistently among the top genera as well showing minimal compression and elongation. Similarly, genus *Leiurus* showed the most anterior tapering of the sternum and *Microbuthus* exhibited the most coxal elongation. For leg coxae elongation, *Microbuthus* reflected the highest value for both coxae III and IV across the 89 genera examined for this paper, including *type 2* sternum scorpions. Considering rankings across all four ratios, *Karasbergia* and *Microtityus* reflect the least overall compression and coxae elongation of the genera examined, while *Leiurus* and *Microbuthus* showed the most compression and elongation.

Although there may be no direct connection between narrowing sternums and the elongation of leg coxae, the statistical data does imply there is some relationship, since out of twenty rankings (the top and bottom ten), eleven genera consistently rank across all four ratios. We can conclude that coxae elongation for legs III and IV is, in part, caused by the narrowing of the sternum, although it is clear, based on all data, that the buthoid leg coxae III and IV are elongated in general. This is apparent by simple inspection of the sternocoxal areas illustrated in Figs. 3-4.
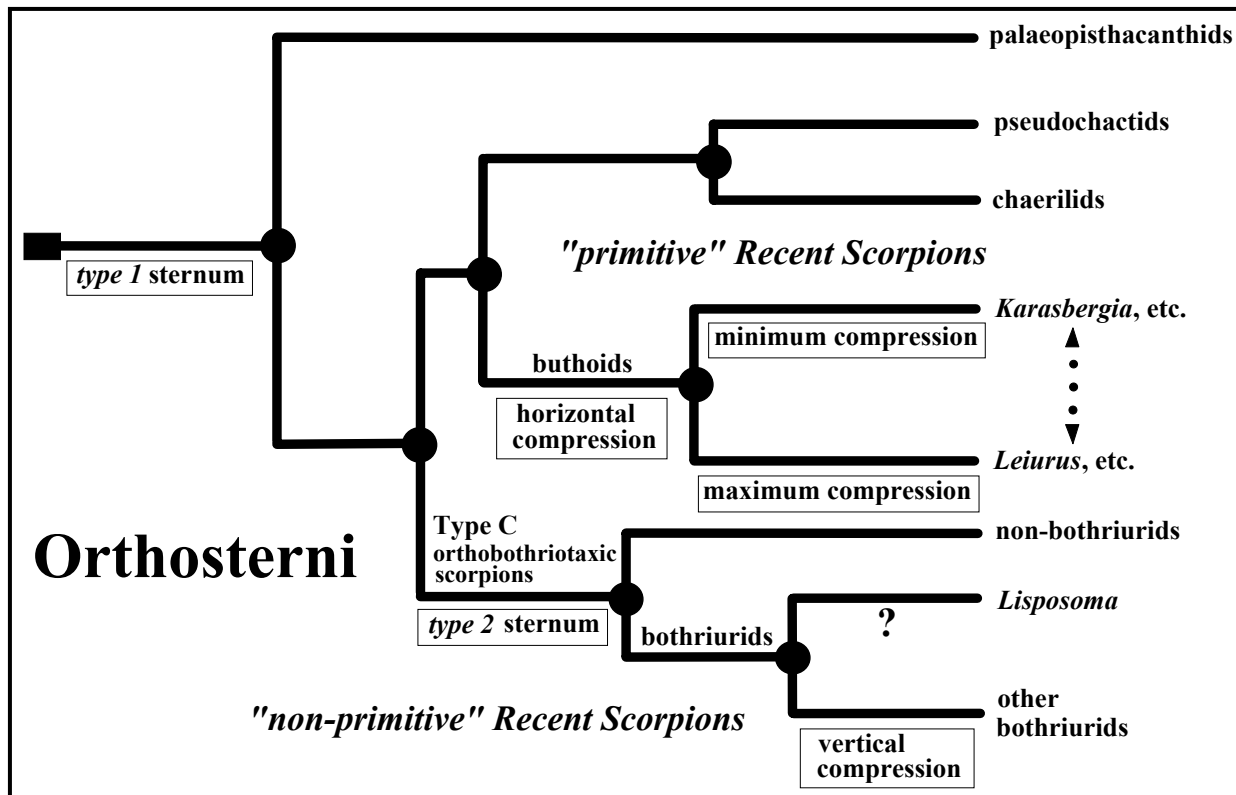
Figure 44: Charogram showing hypothesized evolution of the scorpion *sternum* for infraorder Orthosterni. Character derivations are depicted on the bottom of the branches (enclosed in rectangles) and subclades and taxa are shown on the top of branches or as terminal nodes. *Type 1* sterna is considered plesiomorphic to all Recent scorpions being established for the palaeopisthacanthids; all *type 1* sterna Recent taxa are depicted as "primitive" and *type 2* sterna taxa, globally identified as those scorpions complying to Type C orthobothriotaxy, are considered "non-primitive". We suggest all buthoid scorpions exhibit some degree of horizontal compression, but in highly variable degrees. It is unknown whether the bothriurid genus *Lisposoma* shows vertical compression, so it is depicted separate from the bothriurids proper which exhibit vertical compression.

Phylogenetic and Taxonomic Considerations

We have defined and described in this paper two fundamental sternum types for the scorpion infraorder Orthosterni. Sternum *type 1* is defined for the fossil scorpion *Palaeopisthacanthus* (family Palaeopisthacanthidae) and Recent scorpion families/superfamilies Pseudochactidae, Chaerilidae and Buthoidea. Sternum *type 2* is found in all other Recent scorpions. Interestingly, in literature sterna *type 1* scorpions usually are considered primitive in contrast to sterna *type 2* scorpions which are typically declared as "non-primitive". This important taxonomic structure has been long obscured and misinterpreted for well over one hundred years, involving overzealous interpretations of its "shape". Clearly, as evidenced in the body of this paper, in the large taxonomic picture, the shape of the sternum as well as its gross morphometric proportions are meaningless. Instead, one must look closely at the *actual substructures* that are present in the sternum in order to quantify it and establish meaningful homologies for subsequent cladistic analysis. As established in our study,

this can be accomplished by considering both its external and internal structure.

Phylogenetic considerations

Fig. 44 shows the hypothesized evolution of the scorpion sternum for infraorder Orthosterni in the form of a "charogram". For the purposes of this paper, we hypothesize that sternum *type 1* is derived for the Orthosterni, having been assigned to *Palaeopisthacanthus* (Fig. 3), and therefore is plesiomorphic to all Recent scorpions. However, it is not clear when this sternum type first occurred in this evolutionary lineage. As discussed elsewhere in this paper, based on Kjellesvig-Waering's (1986) description of the sternum of several genera in his superfamily Eoctonoidea, we see that two of these genera exhibit a primitive *type 1* sternum (*Eoctonus* and *Buthiscorpius*), another genus possibly with this type (*Anthracoscorpio*) and a fourth genus with a "triangular" shaped sternum (*Coseleyscorpio*), conceivably similar to that exhibited in the buthoids. Considering Stockwell's (1989: 178-180, Fig. 250) classifi-

cation, the superfamily Eoctonoidea as originally declared by Kjellesvig-Waering (1986) is the infraorder Palaeosterni, the sister group to Orthosterni. Based on these observations it is not unreasonable to suggest that the *type 1* sternum may be a synapomorphy for the suborder Neoscorpionina thus being plesiomorphic for the Orthosterni.

It is clear that this sternum type has not gone through much change in the pseudochactids and, in most part, the chaerilids as well. For *type 1* sterna, the horizontally compressed form found in the buthoids is derived, thus clearly autapomorphic. This conclusion is not new as Stockwell (1989) also considered the "subtriangular" sternum autapomorphic within the buthids (his character 28). Within the buthoids, we see a wide spectrum of compression in the sternum, from little compression as exhibited by those taxa with less elongated and narrow sterna, reflecting the more conventional "pentagonal" form, to those that are truly narrowed anteriorly. In a cladistic sense, it might be prudent to establish compression thresholds dividing the buthoid genera into two, three, or more categories, depicting degrees such as little or no compression, medium compression to considerable compression, etc. (as, for example, adopted in Table 2). Although these categories (or more appropriately in a cladistic sense, character states) may prove to be superficial, other characters may help to determine their legitimacy. For example, by combining these compression states with other characters, excessive homoplasy would imply that homology based on these states is probably superficial. On the other hand, if homoplasy is minimal thus exhibiting some level of synapomorphic potential, then possibly the less compressed taxa (i.e., *Karasbergia*) may prove to be a more primitive form of buthid, implying that buthoids showing the most sternal compression may be more "recently" derived.

The remainder of Recent scorpions conform to *type 2* sterna, which we suggest, as shown in Fig. 44, is derived from the *type 1* sternum. This derivation, which is presumably somewhat complicated based on the differences between the two sternum types, involves primarily the bifurcation of the posterior edge of the sternum. One would suspect that this bifurcation originated from the posterior depression found in *type 1* sterna, since it involves the posterior medial area of the sternum. Internally we see that the posterior depression, represented by a singular rounded process in *type 1* sterna, is bifurcated as well, into two processes which essentially outline the internal aspects of the lateral lobes. The lateral lobes, which can be conspicuously convex, are another significant fallout of this derivation. We suggest here their convex form is a direct result of the bifurcation and, consequently, the apex is considerably depressed in those scorpion groups which exhibit highly convex lateral lobes. It is also important to note here that all *type 2* sterna scorpions are restricted to Type C orthobothrio-

taxy, while *type 1* sterna are found in Types A, B, D, and P orthobothriotaxic scorpions (see Vachon, 1974, and Soleglad & Fet, 2001, for a description of these types).

Within sternum *type 2* we have the highly vertically compressed sternum exhibited in the bothriurids. As discussed in this paper, this sternum compression can be quantified both externally as well as internally. It is important to note that the flattened, partially coalesced internal processes found in the New World bothriurids is also present in the Old World genus *Cercophonius*. We suggest here, based on the length of the internal processes (see Figs. 25, 40-41) that the bothriurid sternum evolved from a sternum with well developed internal processes. Since we have not examined all bothriurid genera, it remains to be determined whether the bothriurids exhibit degrees of compression as witnessed in the buthoids. For example, the "slit-like (= transverse)" vs. "subpentagonal" dichotomy is perpetuated in the key to bothriurid genera provided by Sissom (1990: 87), stating that genus *Tehuankea* has a "subpentagonal" sternum, forming a couplet with *Lisposoma*. Prendini (2000: Table 3) disagreed with this assertion, in part, coding *Tehuankea* as "transverse" while agreeing with Sissom with respect to *Lisposoma*. Prendini (2000: 40-41) examined two *Lisposoma* species; however, he did not have an actual specimen of *Tehuankea* to examine thus based his analysis on exisiting literature. In Cekalovic's (1973: Fig. 21) illustration of the sternum, we see a sternum very similar in structure and proportions to that of *Caraboctonus* (Fig. 8) and *Superstitionia* (Figs. 8 and 9). In this detailed illustration the lateral lobes are not conspicuously separated, but its apex is somewhat flat. We would suspect, based on these intermediate tendencies, that its internal processes will show modest compression, as for example, depicted in Fig. 43. Although *Tehuankea* is reported to have the most "subpentagonal" sternum of the New World bothriurids (L. Acosta, personal communication), we will follow Prendini's cladistic analysis and consider it as "typical bothriurid". In addition, in support of this decision, *Tehuankea* falls well inside the New World bothriurids, not showing a close affinity to *Lisposoma* in Prendini's (2000, Fig. 2) analysis. It remains to be seen if the bothriurid *Lisposoma* (an African taxon) has this unique derivation of the internal processes. Prendini (2000: 48) reports that the *Lisposoma* sternum is "subpentagonal", not "transverse" as typically found in the bothriurids. This is also reported by Lawrence (1927: Fig. 52) and Francke (1982: 36). However, these observations are essentially based on shape and gross proportional criteria, not on fundamental structures of the sternum as described in this study. The illustration provided by Lawrence (1927) does not help us here, since it is a sketch-like outline showing no details of the sternum's surface. Prendini further suggests that the "transverse" sternum of the bothriurids derived after its split from *Lisposoma*. We

adopt this interpretation as well for two reasons: first, it seems reasonable that *Lisposoma* may exhibit some structural separation from the main bothriurid complex considering their biogeographic difference; and, second, since we have not seen the *Lisposoma* sternum and there is no good illustration of it in the literature, we can't verify the finer configurations of the lateral lobes indicating vertical compression. It remains to be seen if *Lisposoma* has the separated lateral lobes and/or a flattened internal processes as exhibited in the true bothriurid sternum. If it does not, then it is clear that Prendini (2000) is correct in his interpretation and the cladogram presented in his Figure 2 showing *Lisposoma* as the plesiomorphic sister genus to the other bothriurids is a reasonable result.

For non-compressed *Type 2* sterna the relative development of the internal processes may provide further characters for taxonomic separation. For example, in the genera *Hadrurus* and *Hadruroides*, we see very elongated processes forming a conspicuous fork-like arrangement distally. The ischnurids have very reduced internal processes consistent with the subtle development of the lateral lobes, *Liocheles* exhibiting the least development. Morphometric ratios may provide possible characters as well, especially in those groups that consistently emphasize a trend such as the longer than wide sternum of the scorpiopines and the subtle narrowing of the posterior aspect of the sternum as seen in the ischnurids and hemiscorpiids.

Taxonomic considerations

In this section we describe in detail the sternum structure of the major scorpion groups analyzed in this study. Although much of this data is based on the examination of a solitary species of a genus, we believe its totality does provide ample evidence for the legitimacy of the two fundamental sternum types proposed in this paper. Hopefully, these descriptions will provide additional data at the lower taxonomic levels for some of these groups, and provide a more precise statement of structure for cladistic analysis. These descriptions include both external and internal substructures. For internal considerations, see **Methods & Material** section for actual taxa dissected.

Pseudochactidae (Figs. 2-3, 14): sternum *type 1* — *External aspect*: horizontal compression absent, lateral sides essentially parallel, showing slightly longer than wide proportions; posterior depression quite reduced, defined posteriorly by slight outer ridge; surface essentially flat, lacking any indication of a concave region or median furrow. *Internal aspect*: essentially flat, lacking any significant three dimensional form; single internal process quite reduced, mirroring its external form. *Comments:* External and internal structures verified in one species (family is monotypic).

Chaerilidae (Figs. 3, 15, 34-35): sternum *type 1* — *External aspect*: horizontal compression weak, lateral sides essentially parallel, showing slightly longer than wide proportions; posterior depression well developed, defined posteriorly by slight outer ridge, and flaring out wider and shallower in an anterior direction; surface evidencing subtle three dimensionality with a slight concave region extending from the posterior depression anteriorly, no median furrow is present. *Internal aspect*: showing a subtle three dimensional form; single internal process quite well developed, extending internally slightly beyond the posterior edge of the sternum, becoming wider and reduced in size anteriorly. *Comments:* external structure verified in three species, internal structures verified in one species (family is monotypic).

Buthidae (Figs. 2-4, 16-19, 36-37): sternum *type 1* — *External aspect*: horizontal compression present, in modest to highly exaggerated forms, lateral sides usually much longer than apex lateral sides, but this is highly variable depending on the degree of compression present; posterior depression usually well developed, forming anywhere from a narrow deep depression to a wider form, defined posteriorly by a well defined outer ridge, sometimes extending along the lateral sides; surface showing considerable three dimensionality, the concave region weak to a deep area occupying the primary posterior medial area; median furrow present on some genera. *Internal aspect*: usually exhibiting significant three dimensional form; single internal process well developed, quite rounded at its extremity. *Comments:* external structure verified in 29 genera, internal verified in nine genera, including both Old and New World genera.

Microcharmidae (Fig. 3): sternum *type 1* — *External aspect*: horizontal compression modest, lateral sides essentially parallel; posterior depression modest and wide posteriorly, defined posteriorly by outer ridge; surface essentially flat, concave region restricted to posterior depression, no median furrow. *Internal aspect*: unknown. *Comments:* external structure verified in one genus. The genera associated with family Microcharmidae have gone through significant revision during this family's short existence (Lourenço, 1995, 1998, 2000b). At the time of this writing Lourenço (2000b) considers two genera valid members of this family, *Microcharmus* and *Neoprotobuthus*. Originally, *Akentrobuthus* (Lourenço, 1998) was placed in this family, but was removed and *Neoprotobuthus* added by Lourenço (2000b). *Microcharmus* was described by Lourenço in 1995.

Iuridae (Figs. 2, 8, 20-21, 38-39): sternum *type 2* — *External aspect:* vertical compression absent, overall proportions are variable, essentially from wide as long to wider than long; apex width slightly narrower than posterior width; posterior emargination quite well developed exhibiting medium to highly convexed lateral lobes and a deep apical depression. *Internal:* internal proc-

esses, which extend the entire length of the inner aspects of the lateral lobes, are very well developed, extending considerably into the scorpion's body. *Comments:* external structure verified in all five genera (*Anuroctonus* is excluded here, see Chactidae), internal structure verified in four genera (*Calchas* was not dissected).

Bothriuridae (Figs. 2, 5, 25, 40-41): sternum *type 2 — External aspect:* vertical compression present, sternum much wider than long; apex width equal to or slightly narrower than posterior width with elongated lateral sides; posterior emargination quite well developed exhibiting medium convexed lateral lobes that are conspicuously separated and abut leg coxae II, and a deep flat apical depression which is widened due to the compression. *Internal:* internal processes are very well developed, considerably flattened and partially coalesced, extending well into the scorpion's body. *Comments:* external and internal structure verified in seven genera, six New World and one Old World.

Scorpionidae (Figs. 5, 22): sternum *type 2 — External aspect:* vertical compression absent, sternum longer than wide to equal in proportions; apex width slightly narrower than posterior width; posterior emargination modestly developed exhibiting somewhat weakly developed convexed lateral lobes; apical depression is weak. *Internal:* internal processes, which extend the entire length of the inner aspects of the lateral lobes, are well developed, extending into the scorpion body. *Comments:* external structure verified in all four genera, internal structure verified in two genera.

Diplocentridae (Figs. 5, 23): sternum *type 2 — External aspect:* vertical compression absent, sternum longer than wide; apex width and posterior width essentially the same; posterior emargination modestly developed exhibiting somewhat weakly developed convexed lateral lobes; apical depression is weak. *Internal:* internal processes, which extend the entire length of the inner aspects of the lateral lobes, are well developed, extending into the scorpion body. *Comments:* external structure verified in five genera, internal structure verified in two genera.

Urodacidae (Fig. 5): sternum *type 2 — External aspect:* vertical compression absent, sternum wider than long; apex width slightly narrower than posterior width; posterior emargination modestly developed exhibiting somewhat weakly developed convexed lateral lobes; apical depression is weak. *Internal:* internal processes, which extend the entire length of the inner aspects of the lateral lobes, are of modest development, extending slightly into the scorpion body. *Comments:* external and internal structure verified in one genus (family is monotypic).

Ischnuridae (Figs. 5, 24): sternum *type 2 — External aspect:* vertical compression absent, sternum slightly longer than wide or equal in proportions; apex width wider than posterior width; posterior emargination

weakly developed exhibiting very weakly developed convexed lateral lobes; apical depression is weak to nonexistent. *Internal:* internal processes, which are present on either entire length of the inner aspects of the lateral lobes or only present posteriorly, are weak, not extending into the scorpion's body. On genus *Liocheles*, the internal processes are reduced to a set of small pigmented posterior granules. *Comments:* external and internal structure verified in four genera.

Hemiscorpiidae (Fig. 5): sternum *type 2 — External aspect:* vertical compression absent, sternum much longer than wide; apex width wider than posterior width; posterior emargination weakly developed exhibiting weak convexed lateral lobes; apical depression is weak to nonexistent. *Internal:* Unknown. *Comments:* external structure verified in one genus.

Euscorpiidae (Figs. 6, 26-27): sternum *type 2 — External aspect:* vertical compression absent, sternum proportions variable, longer than wide to wider than long; apex width narrower than posterior width; posterior emargination well developed exhibiting modest to well developed convexed lateral lobes; apical depression weak to well developed. *Internal:* internal processes, which extend the entire length of the inner aspects of the lateral lobes, are well developed extending well into the scorpion's body. *Comments:* external structure verified on nine genera, internal structure verified in two genera.

Chactidae (Figs. 6, 28-29): sternum *type 2 — External aspect:* vertical compression absent, sternum wider than long or equal; apex width narrower than posterior width; posterior emargination well developed exhibiting modest to well developed convexed lateral lobes; apical depression weak to well developed. *Internal:* internal processes, which extend the entire length of the inner aspects of the lateral lobes, are well developed extending well into the scorpion's body. *Comments:* external structure verified in nine genera (which includes *Anuroctonus* and *Belisarius*), internal structure verified in four genera.

Vaejovidae (Figs. 7, 30-32): sternum *type 2 — External aspect:* vertical compression absent, sternum wider than long; apex width narrower than posterior width; posterior emargination well developed exhibiting modest to well developed convexed lateral lobes; apical depression well developed. *Internal:* internal processes, which extend the entire length of the inner aspects of the lateral lobes, are well developed extending well into the scorpion's body. *Comments:* external structure verified in 13 genera, internal structure verified in eight genera.

Superstitioniidae (Figs. 8, 9-13, 33): sternum *type 2 — External aspect:* vertical compression absent, sternum proportions variable, wider than long, equal or longer than wide; apex width narrower than posterior width; posterior emargination variable, well developed exhibiting modest to well developed convexed lateral lobes to almost nonexistent; apical depression well de-

veloped to obsolete. *Internal:* internal processes, which extend the entire length of the inner aspects of the lateral lobes, are well developed extending well into the scorpion's body. *Comments:* external structure verified in four genera (two from literature), internal structure verified in one genus (*Superstitionia*). Scorpions of this somewhat diverse scorpion family present a wide spectrum of versions of the *type 2* sternum, with *Superstitionia* exhibiting the typical well developed posterior emargination, lateral lobes and internal processes, to the troglobitic genera, *Alacran*, *Typhlochactas* and *Sotanochactas*, which exhibit highly simplified sterna (internal structure unknown). One must assume that adaptation to cave life has caused this simplification to one degree or another, especially the typhlochactines, which are highly cave adapted.

Acknowledgements

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