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Systematics and biogeography of the family Scorpionidae (Chelicerata: Scorpiones), with a discussion on phylogenetic methods

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Abstract. A cladistic analysis of relationships among the genera of Scorpionidae Latreille, 1802—*Heterometrus* Ehrenberg, 1828; *Opistophthalmus* C. L. Koch, 1837; *Pandinus* Thorell, 1876; and *Scorpio* Linnaeus, 1758—based on morphology and DNA sequence data from loci of three genes in the mitochondrial genome (12S ribosomal DNA (rDNA), 16S rDNA and cytochrome oxidase I) and one gene in the nuclear genome (28S rDNA) is presented. The analysis makes use of exemplar species, specifically selected to test the monophyly of the genera, rather than supraspecific terminal taxa. Other methods used in the analysis are justified in the context of a discussion of current methods for phylogenetic reconstruction. Relationships among the scorpionid genera are demonstrated to be as follows: (*Opistophthalmus* (*Scorpio* (*Heterometrus* + *Pandinus*))). This reconstruction identifies *Opistophthalmus* as the basal lineage of the Scorpionidae, rather than the sister-group of *Scorpio*. Revised descriptions, diagnoses and a key to identification of the four scorpionid genera are provided, together with a summary of what is known about their ecology, distribution and conservation status.

Introduction

Latreille's (1802) 'Famille des Scorpionides', which included all scorpions, was introduced at the time when strict definitions of order and family were not yet followed (Fet 2000). Subsequent authors divided the order into families, thereby reducing the scope of the Scorpionidae Latreille, 1802 (Table 1). Pocock (1893) first recognised the following subfamilies in the Scorpionidae: Diplocentrini, Hemiscorpiini, Ischnurini, Scorpionini and Urodacini. The Ischnuridae, originally regarded as a separate family by Simon (1879), were retained as a subfamily of the Scorpionidae by all authors subsequent to Pocock (1893), until reinstated as a family by Lourenço (1989). The Diplocentridae were first elevated to family rank by Kraepelin (1905), who also added the subfamily Heteroscorpioninae to the Scorpionidae. Lourenço (1996) later elevated the Heteroscorpioninae to family rank. Lawrence (1928) added the subfamily Lisposominae Lawrence, 1928, which was transferred to the Bothriuridae Simon, 1880 by Francke (1982*a*).

Before the cladistic analyses of Stockwell (1989) and Prendini (2000*a*), the Scorpionidae included, by default, three subfamilies remaining from Pocock's (1893, 1900*a*) classification: Hemiscorpiinae, Scorpioninae and Urodacinae. In the absence of any published revisions, both Sissom (1990) and Fet (2000) followed this treatment, although they acknowledged that it was unsatisfactory. Stockwell (1989) had previously proposed that the Hemiscorpiinae be regarded as a subfamily of the Ischnuridae and that the Urodacinae be elevated to family rank, thereby restricting the Scorpionidae to the genera comprising the nominal subfamily (Fig. 1*A*), but his cladistic analysis and revised classification were never published. Lourenço (1996, 2000) concurred with Stockwell's (1989) suggestion to elevate the Urodacinae, but did not publish a formal revision either. It was only after a cladistic analysis demonstrated that not only the Urodacinae, but also the Hemiscorpiinae, should be elevated to family rank, that these emendations were formally implemented (Prendini 2000*a*; Fig. 1*B*). As redefined, the Scorpionidae comprises only the four genera traditionally regarded as the subfamily Scorpioninae: *Heterometrus*, *Opistophthalmus*, *Pandinus* and *Scorpio* (Fig. 2). Lourenço's (1999) recent proposal to transfer the ischnurid genus *Hadogenes* to the Scorpionidae is unsupported by cladistic analysis, as argued elsewhere (Prendini 2001*a*). Lourenço's (2000) creation of the

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monotypic family Lisposomidae, to accommodate the enigmatic *Lisposoma* Lawrence, 1928 (originally placed in the Scorpionidae), is similarly unjustified by the available evidence, which instead suggests that it is a basal bothriurid (Prendini 2000*a*, 2003).

The Scorpionidae is geographically restricted to the Old World (Fig. 3; Table 2) and represents a conspicuous component of the fossorial arthropod fauna throughout Africa (excluding the Sahara), the Middle East, the Indian subcontinent, the South-East Asian mainland and the Indonesian archipelago. Scorpionids are mostly of moderate to large size (70–120 mm in total length) but the family also includes some of the largest extant scorpions, reaching lengths of 160–200 mm (Vachon 1952*b*; Lamoral 1979; Couzijn 1981; Newlands 1987; Sissom 1990). Scorpionids rank among the most long-lived of terrestrial arthropods, with an estimated longevity of 25–30 years for the larger species (Polis and Sissom 1990). In addition to their often large size, most scorpionids display other typical *K*-selected traits, including iteroparity, small broods, protracted development and parental care. Juveniles are altricial, remaining in the natal burrow for several months, where they feed upon prey captured by their mother (Schultze 1927; Shachak and Brand 1983; Polis and Lourenço 1986; Mahsberg 1990; Shivashankar 1994; Crucitti 1999). Scorpionids also appear to be very sensitive to

Table 1. Historical classifications of the family Scorpionidae Latreille

Peters (1861)
- Scorpionini: *Diplocentrus* Peters, 1861; *Hemiscorpius* Peters, 1861; *Heterometrus* Ehrenberg, 1828; *Liocheles* Sundevall, 1833; *Opisthacanthus* Peters, 1861

Thorell (1876*a*) and Karsch (1879*a*, 1879*b*)
- Pandinoidae Thorell, 1876
  - Iurini Thorell, 1876: *Chaerilus* Simon, 1877; *Iurus* Thorell, 1876; *Scorpiops* Peters, 1861; *Uroctonus* Thorell, 1876
  - Pandinini: *Brotheas* C. L. Koch, 1837; *Chactas* Gervais, 1844; *Diplocentrus*; *Euscorpius* Thorell, 1876; *Hemiscorpius*; *Heterometrus*; *Liocheles*; *Nebo* Simon, 1878; *Opisthacanthus*; *Opistophthalmus* C. L. Koch, 1837; *Pandinus* Thorell, 1876; *Scorpio* Linnaeus, 1758; *Urodacus* Peters, 1861

Simon (1879, 1880)
- Heterometridae Simon, 1879: *Heterometrus*; *Iurus*; *Nebo*; *Opistophthalmus*; *Scorpio*

Pocock (1893)
- Scorpionidae
  - Diplocentrini Karsch, 1880: *Diplocentrus*; *Oiclus* Simon, 1880; *Nebo*
  - Hemiscorpiini Pocock, 1893: *Hemiscorpius*
  - Ischnurini Simon, 1879: *Cheloctonus* Pocock, 1892; *Chiromachus* Pocock, 1893; *Iomachus* Pocock, 1893; *Liocheles*; *Opisthocentrus* Pocock, 1893; *Opisthacanthus*
  - Scorpionini: *Heterometrus*; *Opistophthalmus*; *Pandinus*; *Scorpio*
  - Urodacini Pocock, 1893: *Urodacus*

Kraepelin (1894, 1899, 1905)
- Scorpionidae
  - Hemiscorpiinae: *Hemiscorpius*
  - Heteroscorpioninae Kraepelin, 1905: *Heteroscorpion* Birula, 1903
  - Hormurinae Laurie, 1896: *Iomachus*; *Liocheles*
  - Ischnurinae: *Cheloctonus*; *Hadogenes* Kraepelin, 1894; *Liocheles*; *Opisthacanthus*
  - Scorpioninae: *Heterometrus*; *Opistophthalmus*; *Pandinus*; *Scorpio*
  - Urodacinae: *Urodacus*

Birula (1917*a*, 1917*b*)
- Scorpionidae
  - Ischnuraria
    - Hemiscorpiinae: *Hemiscorpius*
    - Heteroscorpioninae: *Heteroscorpion*
    - Hormurinae: *Iomachus*; *Liocheles*
    - Ischnurinae: *Cheloctonus*; *Chiromachetes* Pocock, 1899; *Hadogenes*; *Liocheles*; *Opisthacanthus*
  - Scorpionaria
    - Scorpioninae: *Heterometrus*; *Opistophthalmus*; *Pandinus*; *Scorpio*
    - Urodacinae: *Urodacus*

Sissom (1990) and Fet (2000)
- Scorpionidae
  - Hemiscorpiinae: *Habibiella* Vachon, 1974; *Hemiscorpius*
  - Scorpioninae: *Heterometrus*; *Opistophthalmus*; *Pandinus*; *Scorpio*
  - Urodacinae: *Urodacus*

Stockwell (1989), Prendini (2000*a*) and Lourenço (2000)
- Scorpionidae: *Heterometrus*; *Opistophthalmus*; *Pandinus*; *Scorpio*

environmental degradation and may be regarded as equilibrium species.

A characteristic feature of many scorpionids is their ability to construct burrows in the substratum (Purcell 1899; Skaife 1920; Toye 1970; Lawrence 1971, 1973; Newlands 1972*a*, 1972*b*, 1978; Eastwood 1978*a*, 1978*b*; Lamoral 1978*a*, 1979; Shachak and Brand 1983; Kotzman *et al.* 1989; Khatavkar and More 1990; Shivashankar 1992, 1994). The chelicerae and metasoma, especially the spiniform processes on the ventrolateral carinae of segment V, are used to initially loosen the soil (Newlands 1972*a*; Eastwood 1978*b*), whereas the anterior two pairs of legs, armed with retrolateral rows of macrosetae on the tibia, basitarsi and telotarsi, are used to subsequently scrape and rake it out of the burrow (Eastwood 1978*b*; Lamoral 1979).

Burrows vary from shallow scrapes under stones to elaborate, spiralling tunnels reaching depths of more than 1 m below the surface (depending on the species), but are immediately recognisable by their typical oval, reniform or crescent-shaped entrances (Purcell 1899; Newlands 1972*a*, 1972*b*; Eastwood 1978*a*; Lamoral 1979; Crucitti 1999). This unique entrance shape allows scorpionid burrows to be readily distinguished from the burrows of other fossorial arthropods, which usually have round entrances. Occupied scorpionid burrows can often be recognised by the accumulation of a tumulus of excavated soil outside the entrance, which may function to inhibit rainwater from entering the burrow (Shulov and Levy 1978; Polis 1990).

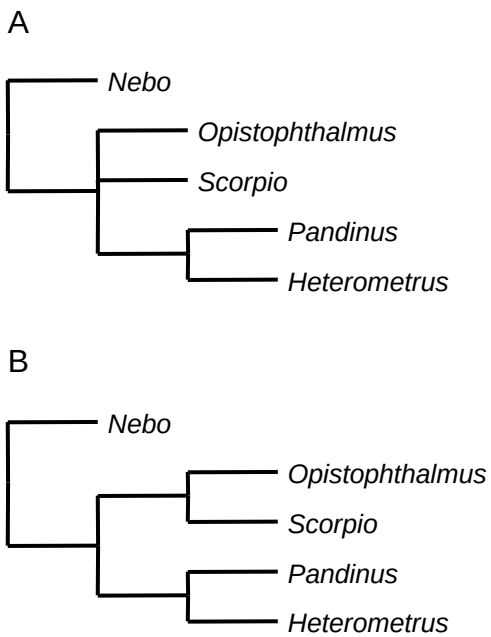

Fig. 1. Previous hypotheses of relationships among scorpionid genera. *A*, The scorpionid section of an unpublished cladogram for the non-buthid genera of Recent scorpions (Stockwell 1989). This tree is part of the strict consensus of 456 MPTs (unweighted length = 208 [*sic*]; *CI* = 66; *RI* = 92) obtained after successive character weighting on 1799 trees (length = 221; *CI* = 62; *RI* = 90). *B*, The scorpionid section of a cladogram for the superfamily Scorpionoidea, based on exemplar species (Prendini 2000*a*). This tree is part of the single MPT (length = 263; *CI* = 55; *RI* = 92) obtained from an analysis with equal weights. Both the analyses of Stockwell (1989) and Prendini (2000*a*) demonstrated the Diplocentridae to be the sister-group of the Scorpionidae, and *Nebo* to be the basal diplocentrid genus, a hypothesis that has received independent corroboration from molecular data (L. Prendini and W. C. Wheeler, unpublished data).

Burrows are constructed by juveniles immediately after departing the natal burrow and appear, in many species, to be occupied for the entire life span of an individual, being enlarged in breadth and depth as the individual grows. The sedentary lifestyle of most scorpionids is evidenced by the dispersion of juvenile burrows around natal burrows, which in many species can be found within a 1–2-m radius thereof. Such low levels of dispersal can result in the formation of dense populations in suitable habitat. For example, *Scorpio maurus palmatus* (Ehrenberg, 1828) reaches densities of 29–54 per 100 m^2 in the Negev Desert of southern Israel (Levy and Amitai 1980; Polis and Lourenço 1986). Low levels of dispersal also represent the evolutionary precursor for advanced subsocial behaviour, which has been documented in some species of *Heterometrus* and *Pandinus* (Polis and Lourenço 1986; Mahsberg 1990; Kriesch 1994; Shivashankar 1994).

As with other obligate fossorial scorpions, the burrow is the location for almost all activities during the life span of an individual scorpionid: feeding, moulting, courtship, copulation, parturition and maternal care (Polis and Sissom 1990). In accordance with their sedentary lifestyle, these scorpions are 'sit-and-wait' or 'ambush' predators (McCormick and Polis 1990). At dusk, individuals emerge from the depths of their burrows to the entrances, remaining there ('doorkeeping') until passing prey comes within range, whereupon they dash out to grab it and then retreat down their burrows to consume it (Toye 1970; Eastwood 1978*a*, 1978*b*; Shachak and Brand 1983; Kotzman *et al.* 1989; Khatavkar and More 1990; Shivashankar 1992, 1994). Given the high densities of scorpionids in some areas, their importance in ecological food webs, particularly with respect to controlling insect populations, is assumed to be considerable.

The Scorpionidae remain poorly studied, despite their widespread distribution and ecological importance. Little or no taxonomic research has been conducted on the four genera in the past 20 years, and nothing whatsoever is known about the ecology of all but a few species. Furthermore, the Scorpionidae are becoming increasingly threatened as habitat destruction continues unabated and new threats (e.g. harvesting for the exotic pet trade) arise. The threats faced by many of these extremely range-restricted scorpions renders the task of inventorying their diversity, distribution and ecology an urgent priority if steps towards their conservation are to be implemented without delay. Attending to this

priority constitutes a prime motivation for a research program into the systematics and biogeography of the Scorpionidae currently underway.

The following contribution presents a cladistic analysis of relationships among the four genera of Scorpionidae, based on morphology and DNA sequence data from loci of three genes in the mitochondrial genome (12S ribosomal DNA (rDNA), 16S rDNA, cytochrome oxidase I) and one gene in the nuclear genome (28S rDNA). This analysis makes use of exemplar species, specifically selected to test the monophyly of the genera, rather than supraspecific terminal taxa (following Prendini 2000*a*, 2001*b*). As a result of this investigation, revised descriptions, diagnoses and a key to identification of the four scorpionid genera are provided, together with a summary of what is known about their ecology, distribution, and conservation status.

Material and methods

Taxa

All four scorpionoid genera were included as ingroup taxa in the present analysis, each of which was represented by at least two exemplar species (Appendix 1). Exemplar species were chosen so as to provide the strongest test of monophyly for the genera they represented. This was achieved by attempting to reflect maximal morphological diversity within the genera, thereby allowing groupings that are largely independent of the *a priori* assumptions encapsulated in the current taxonomy (Prendini 2000*a*, 2001*b*). Type species of each genus were also included as exemplars.

On the basis of these criteria, two Indian and two South-East Asian species of *Heterometrus* were selected, together with four *Opistophthalmus* species from southern, central and eastern Africa, and four *Pandinus* species from western, central and eastern Africa. Two of the nineteen currently recognised subspecies of the monotypic *Scorpio maurus* Linnaeus, 1758 were included as putative phylogenetic species (Nelson and Platnick 1981; Cracraft 1983, 1989; Nixon and Wheeler 1990; Wheeler and Nixon 1990).

Characters were polarised by means of outgroup comparison (Watrous and Wheeler 1981; Farris 1982; Nixon and Carpenter 1993), using the type species of the basal diplocentrid genus, *Nebo*. This decision is justified on the grounds of morphological and molecular evidence that the Diplocentridae are the sister-group of the Scorpionidae (Stockwell 1989; Prendini 2000*a*; L. Prendini and W. C. Wheeler, unpublished data).

The use of an exemplar approach in a previous analysis (Prendini 2000*a*) was recently questioned by Soleglad and Sissom (2001), who stated in their discussion on trichobothrial analysis that ‘the exemplar approach employed in [Prendini’s] analysis probably did not provide enough taxa to ascertain in detail the patterns and extent of

Fig. 2. Representative scorpionids. *A*, *Heterometrus laoticus* Couzin, 1981, ♂ (Vietnam). *B*, *Opistophthalmus boehmi* (Kraepelin, 1897), ♀ (Tanzania). *C*, *Pandinus colei* (Pocock, 1896), ♀ (Ethiopia). *D*, *Scorpio maurus palmatus* (Ehrenberg, 1828), ♂ (Israel).

neobothriotaxic conditions … less than 20% of scorpionoid species were actually evaluated'. Soleglad and Sissom (2001) stated that they studied 33 ingroup species ('over 60%' of ingroup species diversity) for their analysis of euscorpiid phylogeny, yet combined their observations into just 11 supraspecific terminal taxa (hypothetical placeholders for the 11 genera of Euscorpiidae Laurie, 1896), rather than presenting a matrix and analysis of the 33 species that they studied. As argued previously (Prendini 2000*a*, 2001*b*; also see Giribet 2002), there are many theoretical and empirical disadvantages to using supraspecific terminal taxa instead of exemplars. The most obvious that apply to the analysis by Soleglad and Sissom (2001) are: (*1*) the loss of information resulting from the conversion of characters pertaining to 33 species into 11 supraspecific terminals; (*2*) the low potential for repeatability of this process (e.g. it is unclear from Soleglad and Sissom's methodological discussion how decisions regarding character polarity were made, and interspecific variation accommodated, *a priori*); (*3*) the fact that the monophyly of supraspecific taxa (genera) was assumed, rather than tested in the analysis; and (*4*) the implications that this could have for resolving (rather than assuming) the ancestral states of the supraspecific taxa (genera) in the course of a global analysis. The use of supraspecific terminal taxa by Soleglad and Sissom (2001) reduces the explanatory power, and consequently the general utility, of their proposed hypothesis and resultant classification. Their analysis, indeed, contradicts their criticism.

Morphological characters

In an effort to ensure consistent treatment and repeatability, all characters used in the analysis were critically examined in actual specimens. A total of 106 characters (103 characters of the adult morphology and 3 behavioural characters) was scored across the 15 terminal taxa for the cladistic analysis (Table 3; Appendix 2). Of these characters, 58 were compiled from entries in the data matrices of Lamoral (1979), Couzijn (1981) and Prendini (2000*a*). The 48 remaining characters are previously unpublished observations or characters newly coded from the taxonomic literature (and verified by the examination of specimens). Many of these characters (e.g. carapacial sutures, pedipalp trichobothrial patterns, hemispermatophores and colour patterns) were unstudied in the Scorpionidae before this study.

Examination of specimens necessitated a reinterpretation of putative homologies in some characters obtained from the literature, whereas others were modified through addition of new information. Accordingly, some characters were merged, whereas others were split, or particular states thereof transferred to different characters. An attempt was made to avoid *a priori* judgements of character reliability; hence, only characters or character states that were difficult to visualise and score unambiguously were discarded.

Binary and multistate methods were both used in character coding, and an effort was made to code characters in a manner that minimised inapplicable and missing entries (Maddison 1993; Pleijel 1995; Wilkinson 1995; Strong and Lipscomb 1999; Lee and Bryant 1999). Composite coding (*sensu* Maddison 1993; Strong and Lipscomb 1999), in which a character complex is coded into a single multistate character, was used preferentially as a means to this end. Consequently, 71 characters were coded into binary states and 35 were coded into multiple states (Appendix 2). Transformation series could not be inferred for multistate characters, which were therefore treated as unordered, that is, nonadditive (Fitch 1971).

Although most characters were qualitative, several quantitative characters (primarily morphometric ratios and meristic data, e.g. trichobothrial, macrosetal and pectinal tooth counts) were also included. These characters were coded by plotting frequency distributions and, when multimodality was observed, delimiting states according to gaps in the variation ('gap coding'; Mickevich and Johnson 1976; Archie 1985; Felsenstein 1988*a*).

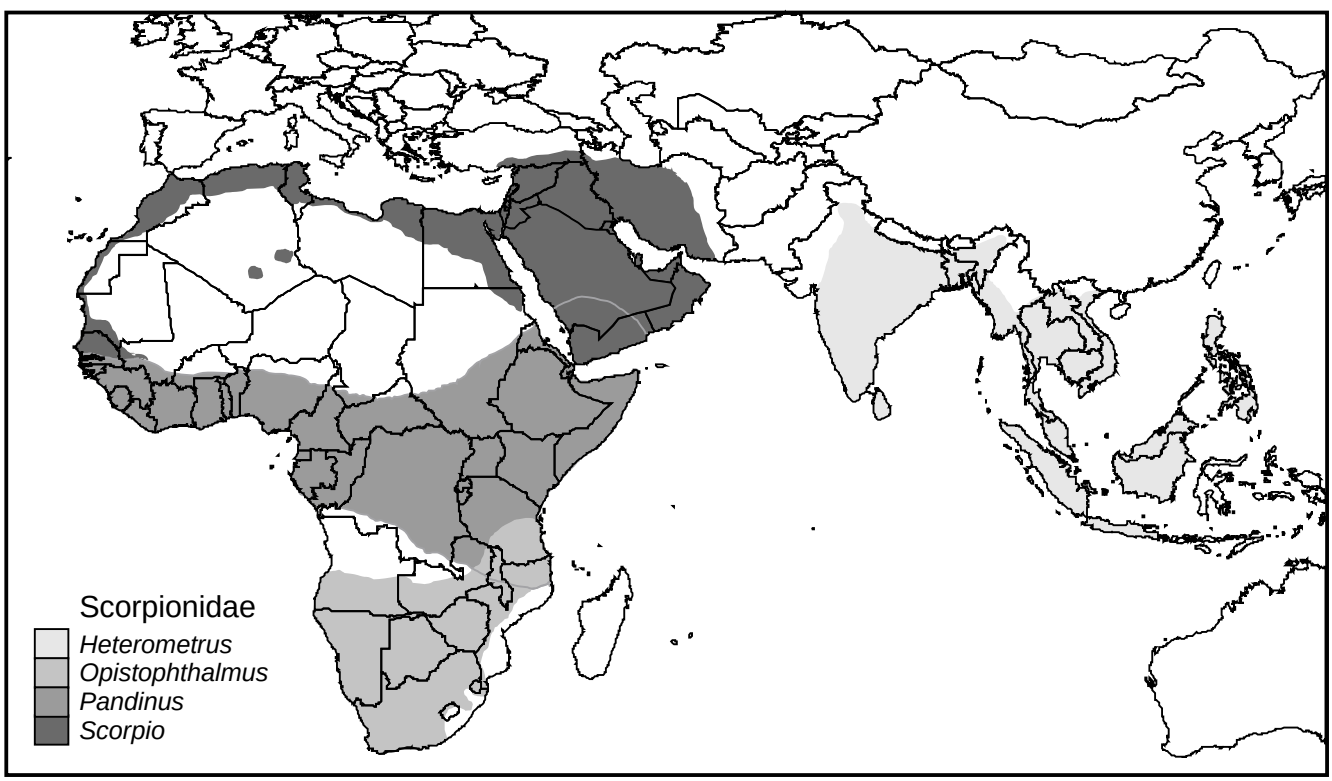

Fig. 3. Approximate global distribution of the four genera in the family Scorpionidae.

Table 2. Countries from which scorpionid genera and species have been recorded, numbers recorded in each, and number of endemic species (parentheses)

Counts for *Heterometrus* and *Scorpio* include subspecies, whereas those for *Opistophthalmus* include as-yet-undescribed species to be recognised in a forthcoming revision (L. Prendini, unpublished data)

Country	*Heterometrus*	*Opistophthalmus*	*Pandinus*	*Scorpio*	Genera	Species
South Africa		52 (40)			1	52 (40)
Namibia		33 (22)			1	33 (22)
India	24 (22)				1	24 (22)
Somalia			17 (9)		1	17 (9)
Indonesia	14 (13)				1	14 (13)
Morocco				10 (8)	1	10 (8)
Philippines	5 (5)				1	5 (5)
Sri Lanka	5 (4)				1	5 (4)
Angola		5 (1)			1	5 (1)
Yemen			2 (1)	2 (1)	2	4 (2)
Algeria				4 (1)	1	4 (1)
Iran				2 (1)	1	2 (1)
Sudan			6	1	2	7
Botswana		7			1	7
Ethiopia			6		1	6
Tanzania		2	3		2	5
Kenya			5		1	5
Mozambique		3	1		2	4
Saudi Arabia			1	3	2	4
Zimbabwe		4			1	4
Zambia		2	1		2	3
Cambodia	3				1	3
Eritrea			3		1	3
Jordan				3	1	3
Syria				3	1	3
Vietnam	3				1	3
Malawi		1	1		2	2
Senegal			1	1	2	2
Democratic Republic of Congo			2		1	2
Guinea			2		1	2
Iraq				2	1	2
Israel				2	1	2
Kuwait				2	1	2
Laos	2				1	2
Libya				2	1	2
Malaysia	2				1	2
Qatar				2	1	2
Singapore	2				1	2
Thailand	2				1	2
Tunisia				2	1	2
Benin			1		1	1
Brunei	1				1	1
Burkina Faso			1		1	1
Cameroon			1		1	1
Central African Republic			1		1	1
Chad			1		1	1
Congo			1		1	1
Côte d'Ivoire			1		1	1
Egypt				1	1	1
Equatorial Guinea			1		1	1
Gabon			1		1	1
Gambia			1		1	1
Ghana			1		1	1
Guinea-Bissau			1		1	1
Lebanon				1	1	1

(*continued next page*)

Table 2. (continued)

Country	*Heterometrus*	*Opistophthalmus*	*Pandinus*	*Scorpio*	Genera	Species
Lesotho		1			1	1
Liberia			1		1	1
Mauritania				1	1	1
Myanmar	1				1	1
Nigeria			1		1	1
Oman				1	1	1
Sierra Leone			1		1	1
Swaziland		1			1	1
Togo			1		1	1
Turkey				1	1	1
?Mali			1		1	1

Morphological terminology follows Vachon (1974) for trichobothrial notation, Couzijn (1976) for segmentation of legs, Hjelle (1990) and Sissom (1990) for segmentation of pedipalps, Prendini (2000*a*) for pedipalp and metasomal carinae, and Stahnke (1970), Lamoral (1979), Couzijn (1981) and Sissom (1990) for remaining features. Colour patterns were defined subjectively by comparing the relative intensity of colour and the presence or absence of infuscation on adjacent segments. Photographs were taken under long-wave ultraviolet light using a Microptics™ ML1000 digital imaging system.

Character data were edited, cladograms prepared, and character optimisations conducted using WinClada, Ver. 0.9.9+ (Nixon 1999*a*). Ambiguous optimisations were mostly resolved using accelerated transformation (ACCTRAN) or Farris optimisation, which favours reversals over parallelisms to explain homoplasy (Farris 1970; Swofford and Maddison 1987, 1992; Maddison and Maddison 1992) and therefore maximises homology (Griswold *et al.* 1998). However, delayed transformation (DELTRAN) or Fitch optimisation was used in some cases. Five uninformative characters (21, 36, 38, 58 and 104) were excluded from all analyses; hence, tree statistics are calculated from phylogenetically informative characters only (Bryant 1995).

Acquisition and preservation of samples for DNA isolation

DNA was isolated from pedipalp or leg muscle tissues dissected from live specimens and fixed in 95–100% ethanol (Fet and Vezzetti 1994; Prendini *et al.* 2002). Live specimens, collected in the field or obtained from colleagues, were usually brought back to the laboratory for tissue fixation at –20°C, as this has been found to significantly increase the yield of high-molecular-weight DNA (Prendini *et al.* 2002). However, when collecting trips endured for more than 14 days, tissues were fixed in the field at ambient temperature. Tissue samples were mostly taken from juveniles and subadults. Adults, collected from the same populations, have been retained as voucher specimens in the collection of the American Museum of Natural History (AMNH), New York. Tissue samples are stored separately (in the vapour phase of liquid nitrogen at –15°C) in the Ambrose Monell Collection for Molecular and Microbial Research at the AMNH (Table 4; Appendix 1).

Choice of gene loci

Because alternative data sources are implicitly excluded when a particular data source (e.g. a set of morphological characters or a gene) is selected for a given study (Nixon and Carpenter 1996*a*; Swofford *et al.* 1996), data source selection should be conducted on the basis of reasoned expectations of the value (in time and money) of the data (Nixon and Carpenter 1996*a*). Regrettably, such decisions are seldom made. For example, although the choice of gene loci is a critical step in any molecular phylogenetic analysis, too many investigators make their selections on the basis of primers that are available and/or capable of amplifying the DNA of their study organisms, without regard for the phylogenetic utility of those loci at their level of interest (Brower and DeSalle 1994; Soltis and Soltis 1998).

It has now become generally accepted that more than one gene locus should be used for phylogenetic reconstruction and that at least one locus should be acquired from the recombinant nuclear genome (Avise 1989; Doyle 1992; Degnan 1993; Brower and DeSalle 1994; Brower *et al.* 1996; Maddison 1997; Doyle and Davis 1998). Four loci were selected for the present investigation, not only because of the availability of primers that could consistently amplify sufficiently large, phylogenetically informative fragments, but also because they have been reported to evolve at different rates and would thus be expected to provide phylogenetic resolution at different, overlapping taxonomic levels (e.g. Simon *et al.* 1994; Hayashi 1996; Wahlberg and Zimmermann 2000; Giribet *et al.* 2001*b*).

A variable fragment (D3 region) of the nuclear large-subunit ribosomal RNA gene (28S rDNA) was chosen, as this was considered sufficiently conserved to be informative at the family–genus level, but not so conserved as to have no variation whatsoever. This fragment, amplified with primers designed by Nunn *et al.* (1996), has been used in various studies of arthropod phylogeny at higher and lower levels (e.g. Hillis and Dixon 1991; Weller *et al.* 1992; Pelandakis and Solignac 1993; Friedrich and Tautz 1995; Hayashi 1996; Wheeler 1997, 1998*a*; Whiting *et al.* 1997; Wheeler and Hayashi 1998; Zrzavý *et al.* 1998*b*, 2001; Edgecombe *et al.* 1999; Giribet *et al.* 1999*a*, 1999*b*, 2001*b*, 2002; Giribet and Ribera 2000; Wheeler *et al.* 2001).

In addition, three genes were selected from the more labile mitochondrial (mt) genome. A fairly conserved fragment of the gene for cytochrome *c* oxidase subunit I (*COI*), corresponding to the region between positions 1539 and 2172 of the *Drosophila yakuba* Burla mt genome (Clary and Wolstenholme 1985), was amplified using two pairs of primers designed by Harrison *et al.* (1987) and Folmer *et al.* (1994). It has been used to determine relationships within Coleoptera, Lepidoptera, Orthoptera and other insect groups (Harrison *et al.* 1987; Simon *et al.* 1994; Wahlberg and Zimmermann 2000; Zimmermann *et al.* 2000) as well as among spiders (Arnedo *et al.* 2002), and was also recently used in a study of arthropod phylogeny (Giribet *et al.* 2001*b*).

Comparatively labile fragments of the mitochondrial homologues of the nuclear large-subunit ribosomal RNA gene (16S rDNA) and the nuclear small-subunit ribosomal RNA gene (12S rDNA), both of which also contain conserved regions, were also chosen. These fragments correspond, respectively, to the regions between positions 12887 and 13398 and positions 14233 and 14588 of the *D. yakuba* mt genome (Clary and Wolstenholme 1985). The 16S fragment, amplified with primers designed by Simon *et al.* (1991), has been employed in various studies of interspecific and intraspecific variation in insects (Xiong and Kocher 1991; Vogler and DeSalle 1993; Vogler *et al.* 1993*a*, 1993*b*; Simon *et al.* 1994; Fang *et al.* 1995; Wahlberg and Zimmermann 2000;

Zimmermann *et al.* 2000) and spiders (Hayashi 1996; Arnedo *et al.* 2002). The same fragment, but approximately 100 base pairs (bp) shorter, was used in recent studies of intraspecific and interspecific variation among the following scorpion taxa: *Buthus occitanus* (Amoreux, 1789) (Gantenbein *et al.* 1999*b*); *Centruroides exilicauda* (Wood, 1863) (Gantenbein *et al.* 2001*a*); *Euscorpius* Thorell, 1876 (Gantenbein *et al.* 1999*a*, 2000*a*, 2001*b*; Scherabon *et al.* 2000); *Hadrurus* Thorell, 1876 (Fet *et al.* 2001); and *Mesobuthus gibbosus* (Brullé, 1832) (Gantenbein *et al.* 2000*b*; Gantenbein and Largiadèr 2002). It was also recently used in studies of arthropod phylogeny (Zrzavý *et al.* 1998*b*; Giribet *et al.* 2001*b*). The 12S fragment, amplified with primers designed by Kocher *et al.* (1989), has been suggested to be slightly more conserved than the 16S fragment, and has been used in studies of the internal relationships of arthropods and insects (e.g. Harrison *et al.* 1987; Ballard *et al.* 1992; Simon *et al.* 1994; Wägele and Stanjek 1995; Zrzavý *et al.* 1998*b*).

DNA isolation, amplification and sequencing

Laboratory work was conducted at the Molecular Systematics Laboratory of the AMNH. Genomic DNA was isolated from ethanol-preserved tissues with homogenisation buffers. Most tissue samples were homogenised in a buffer solution comprising 1 volume (400 μL) of 4 M guanidinium isothiocyanate (5 g mL^{-1} guanidinium thiocyanate, 1 M Tris-Cl, pH 7.5) and 0.14 M β-mercaptoethanol, by agitation for 1–2 h at ambient temperature, following a modified protocol for RNA extraction (Chirgwin *et al.* 1979) used by Edgecombe *et al.* (1999), Giribet *et al.* (1999*a*, 1999*b*) and Giribet and Ribera (2000). Some samples were homogenised in a proteinase buffer solution (10 mM Tris, 25 mM EDTA, 0.5% SDS, 100 mM NaCl, 0.1 mg mL^{-1} proteinase K), by agitation for at least 12 h while incubating at 55°C, following the protocol of Whiting *et al.* (1997). After homogenisation, DNA was cleaned in a standard 25:24:1 phenol–chloroform–iso-amyl alcohol series (Palumbi *et al.* 1991), precipitated in 100% ethanol and 3 M sodium oxaloacetate (pH 5.2), dehydrated in a vacuum at 60°C, and resuspended in water. Tissue samples that proved difficult to amplify during the polymerase chain reaction (PCR) were re-extracted using the Qiagen Dneasy Tissue Kit: Dneasy Protocol for Animal Tissues (Qiagen, Venlo, The Netherlands). Consult Nishiguchi *et al.* (2002) for further details of DNA isolation protocols used in this study.

Double-stranded template, suitable for sequencing, was prepared by PCR amplification with the primers listed in Table 5. Primer pairs 28Sa/b, 12Sai/bi and 16Sar/br were respectively used to amplify fragments of 28S rDNA, 12S rDNA and 16S rDNA, whereas the *COI* fragment was amplified with combinations of the HCO/LCO and

Table 3. Distribution of 106 morphological and behavioural characters among a diplocentrid outgroup and exemplar ingroup taxa chosen for cladistic analysis of the family Scorpionidae

Character states are scored 0–3, ? (unknown) or – (inapplicable). Refer to Appendix 1 for material examined and Appendix 2 for character descriptions

Taxa	Characters										
	1	10	20	30	40	50					
N. hierichonticus	00000	00000	00000	01000	00000	00000	00000	00000	00000	00000	000
H. fulvipes	01000	00001	00001	01101	11200	10111	02000	12120	01110	10220	010
H. laoticus	00000	00001	00100	00011	11200	11011	02110	12121	11110	10221	010
H. spinifer	00000	00001	00100	01111	11200	11011	02110	12121	11110	10221	010
H. swammerdami	11000	00001	00001	02201	11200	10111	02000	12120	01110	10220	010
O. boehmi	01111	00101	00001	02201	12101	00111	01000	12100	00000	11000	010
O. capensis	01111	11112	11010	11100	12101	00111	00101	11111	10000	11001	010
O. carinatus	01111	11111	10010	11100	12110	00110	00000	11110	01000	01001	010
O. holmi	01101	01110	11022	22010	11111	10111	02001	22100	00001	10000	2-0
P. cavimanus	01000	00001	10101	02001	12200	11000	02000	12121	10111	10210	1-1
P. dictator	10000	00001	10000	03301	12200	10111	02000	12121	11111	10210	000
P. imperator	10000	00001	10000	03201	12200	10111	02000	12121	11111	10210	1-1
P. viatoris	01000	00001	10101	02201	12200	11000	02000	12121	10111	10210	1-0
S. maurus fuscus	01001	00001	11000	03000	11101	00111	10000	11111	10000	10110	010
S. maurus palmatus	01001	00001	11000	03000	11101	00111	11000	11101	10000	10110	010
	60	70	80	90	100						
N. hierichonticus	00000	00000	00000	00000	01000	00000	00000	00000	00000	00000	000
H. fulvipes	00011	11101	12020	10000	01100	11000	11000	11002	01021	01000	1?0
H. laoticus	00011	11101	12020	10000	10100	11000	11001	11002	01021	11000	??0
H. spinifer	00011	11101	12020	10000	10100	11000	11001	11002	01021	11000	??0
H. swammerdami	00011	11101	12020	10000	01100	11000	11000	11002	01021	11000	1?0
O. boehmi	10001	00011	21111	01201	01010	11010	00110	11010	11110	00000	110
O. capensis	10001	01000	21230	01111	02101	11101	11000	22112	11121	02211	100
O. carinatus	10001	00000	21111	00001	00011	11100	12000	21112	11020	02001	100
O. holmi	31002	02110	21230	01211	00110	01101	00-00	10010	10100	02222	110
P. cavimanus	12011	01111	12120	10000	01100	00010	10000	11001	01021	10000	??0
P. dictator	12011	01101	12120	10000	01100	11000	11000	11002	01021	11000	?00
P. imperator	22011	01101	12120	10000	01100	11000	11000	11002	01021	11000	?00
P. viatoris	12011	01101	12120	10000	01100	11000	11000	11001	01021	11000	1?0
S. maurus fuscus	00101	01100	21110	00000	01100	00010	00110	01002	01020	00111	101
S. maurus palmatus	00101	01100	21110	00000	01110	00010	00110	10010	10110	00111	111

Table 4. Tissue samples used for DNA isolation from a diplocentrid outgroup and exemplar ingroup taxa chosen for cladistic analysis of the family Scorpionidae

All samples, for which accession numbers are listed, are deposited in the Ambrose Monell Collection for Molecular and Microbial Research (AMCC) at the American Museum of Natural History, New York. Genbank accession codes are provided for the respective sequences

Species	Specimen	Country	AMCC	28S	12S	16S	COI
N. hierichonticus	Juv. ♂	Israel	101694	AY156526	AY156541	AY156556	AY156571
H. fulvipes	♀	India	101695	AY156527	AY156542	AY156557	AY156572
H. laoticus	♀	Vietnam	101697	AY156528	AY156543	AY156558	AY156573
H. spinifer	♂	Singapore	101699	AY156529	AY156544	AY156559	AY156574
H. swammerdami	♂	India	101700	AY156530	AY156545	AY156560	AY156575
O. boehmi	♀	South Africa	100803	AY156531	AY156546	AY156561	AY156576
O. capensis	Juv. ♂	South Africa	100811	AY156532	AY156547	AY156562	AY156577
O. carinatus	♂	South Africa	101708	AY156533	AY156548	AY156563	AY156578
O. holmi	♀	Namibia	100846	AY156534	AY156549	AY156564	AY156579
P. cavimanus	Juv. ♀	Tanzania	101701	AY156535	AY156550	AY156565	AY156580
P. dictator	♀	Gabon	101702	AY156536	AY156551	AY156566	AY156581
P. imperator	♂	Ghana	101703	AY156537	AY156552	AY156567	AY156582
P. viatoris	♂	Tanzania	101704	AY156538	AY156553	AY156568	AY156583
S. maurus fuscus	Subad. ♂	Israel	101705	AY156539	AY156554	AY156569	AY156584
S. maurus palmatus	♀	Egypt	101706	AY156540	AY156555	AY156570	AY156585

C1-J-1718/Nancy primers. Amplification was conducted in a 50-μL volume reaction, with 1.25 U of AmpliTaq DNA Polymerase (Perkin Elmer, Wellesley, MA, USA), 200 μM of dNTPs and 1 μM of each primer, or using Ready-To-Go PCR beads (Amersham Pharmacia Biotech, Piscataway, NJ, USA), to which were added 1 μL per reaction of each 10 μM primer, 23 μL of water, and 2 μL of DNA. The PCR program consisted of an initial denaturing step at 94°C for 5 min, 40 amplification cycles (94°C for 15 s, 49°C for 5 s, 72°C for 15 s), and a final step at 72°C for 7 min in a GeneAmp PCR System 9700 (Perkin Elmer) thermocycler. Specific conditions were optimised for taxa and primer pairs (e.g. a lower annealing temperature was used to amplify the *COI* fragment).

PCR products were verified on 1% agarose/TBE electrophoretic gel, purified with the Geneclean II kit (BIO 101) or the Qiagen Qiaquick 96 PCR Purification Kit, dehydrated in a vacuum at 60°C, and resuspended in 10 μL water. Double-stranded sequencing of the PCR products was conducted by the dideoxy termination method (Sanger *et al.* 1977) using automated Applied Biosystems Inc. (ABI, Foster City, CA, USA) Prism 377 and 3700 DNA sequencers (which read 48 and 96 reactions, respectively).

Cycle-sequencing with AmpliTaq DNA Polymerase FS (Perkin Elmer) using dye-labelled terminators (ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction Kit) was performed in a GeneAmp PCR System 9700 (Perkin Elmer) thermocycler. Cycle-sequencing was conducted in a 10-μL volume reaction, comprising 2 μL of Big Dye, 2 μL of Big Dye Extender, 1 μL of 3.2 μM primer, 3 μL of water and 2 μL of DNA. The cycle-sequencing program consisted of 25 amplification cycles (96°C for 15 s, 50°C for 15 s, 60°C for 4 min).

Dye-labelled cycle-sequence products destined for the 377 DNA sequencer were cleaned by centrifuging through Sephadex columns or by ethanol precipitation: 0.1 volumes of 3 M sodium oxaloacetate (pH 5.2) and 2 volumes of 95% ethanol were added, placed on ice for 10 min, centrifuged for 20 min at 31 444*g*, and cleaned in 50 μL of 70% ethanol. Cleaned products were then dehydrated in a vacuum at 60°C, resuspended in 3 μL loading buffer (1:5 dilution of loading dye in formamide) and loaded manually into the gel.

Products destined for the 3700 DNA sequencer were cleaned by precipitation with isopropanol and ethanol (40 μL 70% isopropanol added; centrifuged for 30 min at 2465*g*; microtitre plate inverted and

Table 5. Primers used in amplification and sequencing of Scorpionidae and Diplocentridae

Further details on the following primer pairs are provided in Simon *et al.* (1994): 12Sai/bi, 16Sar/br, C1-J-1718/Nancy

Primer	Alias	5′–3′	Reference
28Sa	D3A	GACCCGTCTTGAAACACGGA	Nunn *et al.* (1996)
28Sb	D3B	TCGGAAGGAACCAGCTACTA	Nunn *et al.* (1996)
12Sai	SR-N-14588	AAACTAGGATTAGATACCCTATTAT	Kocher *et al.* (1989)
12Sbi	SR-J-14233	AAGAGCGACGGGCGATGTGT	Kocher *et al.* (1989)
16Sar[A]	LR-N-13398	CGCCTGTTTATCAAAAACAT	Simon *et al.* (1991)
16Sbr	LR-J-12887	CTCCGGTTTGAACTCAGATCA	Simon *et al.* (1991)
HCO	HCO2198-N-2175	TAAACTTCAGGGTGACCAAAAAATCA	Folmer *et al.* (1994)
LCO	LCO-1490-J-1514	GGTCAACAAATCATAAAGATATTGG	Folmer *et al.* (1994)
	C1-J-1718	GGAGGATTTGGAAATTGATTAGTTCC	Harrison *et al.* (1987)
Nancy	C1-N-2191	CCCGGTAAAATTAAAATATAAACTTC	Harrison *et al.* (1987)

[A]Gantenbein *et al.* (1999*a*, 1999*b*, 2000*a*, 2001*a*, 2001*b*), Scherabon *et al.* (2000) and Fet *et al.* (2001) used a scorpion-specific primer (5′-GTGCAAAGGTAGCATAATCA-3′) instead of 16Sar, which amplifies a fragment *c.* 80 bp shorter (Prendini 2001*d*).

centrifuged for 1 min at 50*g*; 40 μL 70% ethanol added; and centrifuged for 30 min at 2465*g*), air-dried for 30 min, resuspended in 10 μL formamide and loaded directly (in microtitre plates) onto the 3700 sequencer, four plates at a time.

DNA sequence editing

The accuracy of sequences was verified, in all cases, by independently amplifying and sequencing the complementary strands of all fragments. If complementary strands disagreed (besides minor mismatches), the sample was reamplified and sequenced to resolve discrepancies. Chromatograms obtained from the automated sequencers were edited, primer sequences removed, and consensus sequences created from the complementary strands with Sequence Navigator Ver. 1.0.1 (ABI), Sequencher Ver. 3.0 (Gene Codes Corporation, Ann Arbor, MI, USA) and Chromas Ver. 1.62 (Technelysium, available at http://www.technelysium.com.au/chromas.html).

Sixty sequences were generated for this study. The 28S rDNA and *COI* fragments were exactly 312 and 658 bp, respectively, in all species, whereas the 12S rDNA and 16S rDNA fragments varied from 328 to 335 bp (mean 332, mode 333 bp) and from 481 to 487 bp (mean 483, mode 482 bp), respectively (Table 6). The four fragments comprise a total of 1779–1792 bp per species.

Multiple sequence alignment

As the basis for primary homology statements, on which all subsequent analyses depend, sequence data alignment represents the fulcrum of molecular systematics (Fitch and Smith 1983; Feng and Doolittle 1987; Felsenstein 1988*b*; Mindell 1991; Wheeler 1994; Hillis *et al.* 1996; Doyle and Davis 1998; Giribet and Wheeler 1999; Phillips *et al.* 2000). Although fundamental, alignment does not necessarily yield objective, precise results owing to various computational difficulties, which may be most severe when sequences are of greatly different lengths (Smith *et al.* 1981; Fitch and Smith 1983; Feng and Doolittle 1987, 1990; Hein 1989, 1990, 1998; Waterman *et al.* 1992; Gatesy *et al.* 1993; DeSalle *et al.* 1994; Wheeler 1994; Wheeler *et al.* 1995; Doyle and Davis 1998; Giribet and Wheeler 1999, 2001; Phillips *et al.* 2000). Fortunately, in the present investigation, there was no length variation among the 28S rDNA and *COI* fragments, and little among the 12S rDNA and 16S rDNA fragments, which respectively exhibited length variation of 6 and 7 bp between the shortest and longest sequences. As such, alignment was a fairly trivial exercise.

Manual alignment, in which positional homology is inferred by intuition, inferences from molecular structure, or some combination of the two, has been criticised for lacking objectivity, repeatability and optimality criteria for alignment and data removal (Gatesy *et al.* 1993; Brower and DeSalle 1994; Titus and Frost 1996; Whiting *et al.* 1997; Doyle and Davis 1998). Accordingly, two multiple sequence alignment algorithms, Clustal X (Higgins and Sharp 1988, 1989; Higgins *et al.* 1992; Thompson *et al.* 1994, 1997; Jeanmougin *et al.* 1998) and MALIGN Ver. 2.7 (Wheeler and Gladstein 1994, 1994–2000), were used to align the 12S rDNA and 16S rDNA fragments. Clustal provides a single multiple alignment that is rapidly generated and, for sequences with minimal length variation (as here), reasonably accurate. However, as length variation among the sequences increases, Clustal alignments become increasingly suboptimal and the possibility of non-unique alignments is not considered (Wheeler and Gladstein 1994, 1994–2000; Wheeler *et al.* 1995; Giribet and Ribera 2000). MALIGN is unique among multiple alignment programs because, as in cladistic analysis, parsimony is used as an optimality criterion for selecting an alignment or alignments from among all possible alignments that minimise the cost for a given set of parameter values. Parsimony-based alignment is more accurate, not to mention more in line with cladistic philosophy, at the cost of being considerably more computationally intensive: two levels of heuristics are involved to generate the alignments and to generate the trees on which the alignments are diagnosed. Given the computational time required to align sequences parsimoniously (Wheeler and Gladstein 1994–2000; Slowinski 1998), the variable regions were excised and only these submitted to MALIGN for alignment, after which they were returned to their original positions within the rest of the alignment, a procedure undertaken with GeneDoc Ver. 2.6.001 (Nicholas and Nicholas 1997). This approach was possible only because extremely conserved, unambiguously alignable regions flank the variable regions in both the 12S rDNA and 16S rDNA fragments.

Alignment in MALIGN was performed using three gap:change or insertion:deletion (indel) cost ratios (representing the relative cost of the insertion or deletion of a base versus a base substitution)—2:1, 4:1 and 4:2—chosen because these have been found to minimise incongruence among aligned data sets in arthropods (Wheeler 1995; Giribet and Wheeler 1999). The shortest alignment was then selected from among them for further analysis (following Wahlberg and Zimmermann 2000).

The gap:change cost ratio was specified in MALIGN with the commands **internal** and **matrix** (specifying a Sankoff or 'step' matrix):

internal 2 matrix 0 1 1 1 1 0 1 1 1 1 0 1 1 1 1 0
= gap:change cost of 2:1.

internal 4 matrix 0 1 1 1 1 0 1 1 1 1 0 1 1 1 1 0
= gap:change cost of 4:1.

internal 4 matrix 0 2 1 2 2 0 2 1 1 2 0 2 2 1 2 0
= gap:change cost of 4:2.

Table 6. Length variation in homologous sequences of the 12S rDNA and 16S rDNA genes among four genera of Scorpionidae and the outgroup *Nebo* (Diplocentridae)
Numbers in parentheses refer to the frequencies with which sequence lengths were observed

Genus	*n*	Number of base pairs					
		12S rDNA			16S rDNA		
		Range	Mean	Mode	Range	Mean	Mode
Nebo	1	335	–	–	484	–	–
Heterometrus	4	333–334	333	333 (3)	481–482	482	482 (3)
Pandinus	4	333–334	333	333 (3)	483–487	485	_[A]
Scorpio	2	330	330	–	481–482	–	–
Opistophthalmus	4	328–331	330	330 (2)	484–485	–	_[B]
Total	15	328–335	332	333 (6)	481–487	483	482 (4)

[A]Actual frequency 483, 484, 485, 487.
[B]Actual frequency 484 (2), 485 (2).

Additional commands used for alignment in MALIGN were as follows (Wheeler and Gladstein 1994–2000): **contig**, **score 2**, **atbr**, **tbr**, **ftbr**, **build**, **randorder 5**, **keepaligns 20**, **keeptrees 20**.

contig favours gap insertion to base mismatch when costs are equal, and thus inserts gaps in groups rather than singly.

score 2 specifies the cost regime applied to multiple alignment; the value 2 signifies that the cladogram search will involve multiple trees.

atbr is tree bisection–reconnection (TBR) branch swapping on alignment topology.

tbr is TBR branch-swapping during cladogram search.

ftbr specifies that single-tree TBR precedes multiple-tree TBR.

build is a Wagner-type heuristic for multiple topologies.

randorder 5 randomly reorders sequences five times and repeats alignment each time to avoid local minima.

keepaligns 20 specifies the maximum number (20) of equally costly alignments to retain under **build**.

keeptrees 20 specifies the maximum number (20) of equally costly cladograms to retain and subject to branch swapping under **score 2**.

The aligned sequence data, as used in subsequent analyses, are provided as 'Accessory Material' on the *Invertebrate Systematics* website (http://www.publish.csiro.au/journals/is). MEGA Ver. 2.1 (Kumar *et al.* 2001) was used for molecular sequence analysis, that is, to calculate nucleotide frequencies, number of constant, variable and informative positions, and so on, from the aligned data.

Alternatives to fixed alignment

The widely used approach to analysing sequences of unequal length by first aligning and then subjecting the prealigned sequences to a normal parsimony analysis, as applied here, has come under increasing criticism (Wheeler 1994, 1996, 1998*b*, 1999, 2000, 2001*a*, 2001*b*; Slowinski 1998; Edgecombe *et al.* 1999; Giribet and Wheeler 1999; Giribet and Ribera 2000; Giribet *et al.* 2000, 2001*b*, 2002; Wahlberg and Zimmermann 2000; Giribet 2001). This approach clearly violates the logic of parsimony because whether an indel is postulated depends on the phylogeny in question. As argued by Wheeler (1996, 1998*b*, 1999, 2000, 2001*a*, 2001*b*), a phylogeny should be evaluated according to how many substitutions and how many indels it requires postulating, so that analyses should simultaneously consider the indels and substitutions required by alternative phylogenies, instead of taking them as given.

Two methods are currently available for achieving this objective: 'optimisation alignment' or 'direct optimisation' (Wheeler 1996, 19*b*, 2000, 2001*a*, 2001*b*; Giribet and Wheeler 1999; Giribet 2001; Janies and Wheeler 2001) and 'fixed states optimisation' (Wheeler 1999; 200*a*, 2001*b*; Giribet 2001). The optimisation alignment method has been used in several studies (Chavarría and Carpenter 1994; Hayashi 1996; Wheeler 1997, 1998*a*; Wheeler and Hayashi 1998; Carpenter and Wheeler 1999*a*, 1999*b*; Edgecombe *et al.* 1999; Giribet 1999; Janies and Mooi 1999; Sorenson *et al.* 1999; Giribet and Ribera 2000; Giribet *et al.* 2000, 2001*b*, 2002; Wahlberg and Zimmermann 2000; Fet *et al.* 2001; Wheeler *et al.* 2001), whereas the fixed-states method is newer and has been used in only a single study (Edgecombe *et al.* 1999). Both methods have been demonstrated to yield more congruent results than multiple sequence alignment when using character congruence among partitions as a criterion (Wheeler and Hayashi 1998; Wahlberg and Zimmermann 2000; Wheeler 2000, 2001*a*, 2001*b*; Giribet 2001; Wheeler *et al.* 2001), although exceptions exist (Giribet and Ribera 2000).198

These criticisms of the current paradigm in molecular phylogenetic analysis are endorsed unequivocally by us. Accordingly, direct optimisation on the unaligned sequences was implemented for comparative purposes (details provided below), although, given the trivial amount of length variation among the sequences in the present investigation, results were expected to be similar to those obtained from the analysis of fixed alignments.

Epistemological considerations

In molecular systematics, as in other fields of science, investigators may choose among different methods for data analysis. These include pairwise distance methods, such as neighbour-joining (Saitou and Nei 1987), statistical approaches, such as maximum likelihood (Felsenstein 1973, 1979, 1981*a*, 1981*b*, 1983, 1988*b*, 2001), and cladistic parsimony (Farris 1970, 1983; Kluge 1984). Despite the fact that the various methods differ fundamentally in their underlying assumptions, many molecular systematists publish trees generated using all or a subset thereof, on the pretext of providing a more severe test of their phylogenetic hypotheses (for recent examples of this practice in scorpion molecular systematics, see Gantenbein *et al.* 1999*a*, 1999*b*, 2000*a*, 2001*a*, 2001*b*; Scherabon *et al.* 2000; Fet *et al.* 2001; Huber *et al.* 2001). Apparently, 'pluralism' (Giribet *et al.* 2001*a*) or 'syncretism' (Schuh 2000) is advocated on the grounds that hypotheses are more robust if supported simultaneously by different analytical procedures. In accordance with Giribet*et al.* (2001*a*), we reject this argument. It is false to contend that congruence among phylogenetic reconstructions obtained with different methods increases confidence, because (*1*) methods with widely differing assumptions (e.g. distance *vs* parsimony) should not be expected to yield congruent results in the first place, and (*2*) the only conclusions that can be drawn when the analyses yield incongruent results are precisely that they are based on different assumptions! Thus, far from providing a more severe test, the use of multiple analytical techniques merely suggests indecision as to which methods are most appropriate for the question or failure to comprehend the essential philosophical differences between the various procedures. Given that it is uncritical to use all methods and inconsistent to select a subset, authors should decide *a priori* which method they will use, and justify their choice accordingly.

The present investigation follows the philosophy that, of the current methods of phylogenetic inference, parsimony analysis is unsurpassed for information content, accuracy and robustness (e.g. Farris 1970, 1983; Platnick 1979, 1985; Kluge 1984, 1997*a*, 1999; Williams 1992; Wheeler and Hayashi 1998; Wheeler *et al.* 2001). As with any method, parsimony can fail but, compared with the alternatives, the modelled circumstances under which it fails are simple and well understood (see Felsenstein 1978; Hendy and Penny 1989; Goldman 1990; Swofford and Olsen 1990; Penny *et al.* 1992; Huelsenbeck and Hillis 1993; Steel *et al.* 1993; Zharkikh and Li 1993; Kuhner and Felsenstein 1994, 1995; Takezaki and Nei 1994; Huelsenbeck 1995*a*, 1997; Kim 1996; Nei 1996; Swofford *et al.* 1996, 2001; Lewis 1998; Willson 1999; Steel and Penny 2000).

Pairwise distance methods suffer from most of the flaws inherent in phenetic methods (Farris 1981, 1985, 1986, 1990; Swofford 1981; Penny 1982; Steel *et al.* 1988; Siebert 1992; Farris *et al.* 1996; Hillis 1996; Swofford *et al.* 1996; Goldstein and Specht 1998; but see Felsenstein 1984, 1986, 1988*a*). Despite growing popularity (e.g. see Goldman 1990; Penny *et al.* 1992; Hillis *et al.* 1994; Sidow 1994; Yang 1994, 1996*a*, 1996*b*; Gaut and Lewis 1995; Huelsenbeck 1995*b*; Swofford *et al.* 1996; Huelsenbeck and Crandall 1997; Huelsenbeck and Rannala 1997; Rogers 1997; Lewis 1998; LÏo and Goldman 1998;Yang and Bielawski 2000; de Queiroz and Poe 2001; Whelan *et al.* 2001), maximum likelihood has been criticised on the following grounds: (*1*) the results depend upon a model of molecular evolution assumed *a priori*; (*2*) the fit of the data is sacrificed for conformity to the model; (*3*) in order to simplify analyses, the models used are unrealistic; (*4*) realistic models of morphological evolution are generally unavailable, whereas those that have been proposed correspond to parsimony anyway (e.g. Farris 1986, 1999; Wheeler 1990, 1992; Carpenter 1992, 1994; Siebert 1992; Williams 1992;

Wenzel and Carpenter 1994; Siddall and Kluge 1997; Tuffley and Steel 1997; Wenzel 1997; Goldstein and Specht 1998; Siddall 1998; Siddall and Whiting 1999; Schuh 2000; Farris *et al.* 2001; Kluge 2001; Lewis 2001). The inclusion of morphological data provides further justification for the use of parsimony in the present investigation.

The 'simultaneous analysis' or 'total evidence' approach to analysing molecular and morphological data sets (Patterson 1987; Kluge 1989, 1998; Eernisse and Kluge 1993; Patterson *et al.* 1993; Wheeler *et al.* 1993*a*, 1993*b*, 2001; Chavarría and Carpenter 1994; Vrana *et al.* 1994; Bridge *et al.* 1995; Wheeler 1997, 1998*a*; Whiting *et al.* 1997; Wheeler and Hayashi 1998; Zrzavý *et al.* 1998*a*, 1998*b*, 2001; Edgecombe *et al.* 1999, 2000; Giribet *et al.* 1999*a*, 2000, 2001*b*; Schuh, 2000) is a logical extension of the parsimony criterion (Nixon and Carpenter 1996*a*). The advantages and disadvantages of simultaneous analysis have been thoroughly reviewed (Miyamoto 1985; Crowe 1988; Kluge 1989, 1998; Bull *et al.* 1993; de Queiroz 1993; Eernisse and Kluge 1993; Kluge and Wolf 1993; Chippindale and Wiens 1994; de Queiroz *et al.* 1995; Miyamoto and Fitch 1995; Huelsenbeck *et al.* 1996; Nixon and Carpenter 1996*a*; Page 1996; Larson 1998; Edgecombe *et al.* 1999, 2000; Giribet *et al.* 1999*a*) and shall not be elaborated here. In the present context, the arguments of Nixon and Carpenter (1996*a*) concerning explanatory power, character independence and the emergence of secondary signals are considered sufficient justification for this approach. Besides the obvious advantage of a phylogenetic hypothesis based on all available evidence, the information provided by independent data sets can assist in resolving relationships at different levels in the tree, common signal between them can be amplified, thus reducing noise, and characters included in the combined matrix can be reinterpreted during the analysis, thereby supporting clades that were not present in the partitioned data sets. Separate analyses of the morphological and molecular data were only conducted in order to assess character incongruence by means of the incongruence length difference (ILD; Mickevich and Farris 1981; Farris *et al.* 1994, 1995), discussed further below.

Phylogenetic analysis

Initial analyses of the aligned sequence data, separately and in combination with the morphological data, were conducted under equal weighting—that is, one morphological state change equals one base change, indels (gaps) equal substitutions, transitions equal transversions, and with all codon positions equally weighted—with indels treated as a fifth character state. As argued by others (e.g. Allard and Carpenter 1996; Nixon and Carpenter 1996*a*; Edgecombe *et al.* 2000), equal weighting is the obvious and appropriate starting point for any analysis, while the inclusion of indels is justified in the interests of maximising explanatory power (Giribet and Wheeler 1999; Gatesy and Arctander 2000; Phillips *et al.* 2000; Simmons 2000; Simmons and Ochoterena 2000).

Analyses with equal weighting were conducted using heuristic searches in NONA Ver. 2.0 (Goloboff 1997*a*), according to the following command sequence: **hold10000; hold/10; mult*100;** (hold 10 000 trees in memory; hold 10 starting trees in memory; perform TBR branch swapping on 100 random addition replicates). Additional swapping on up to 1000 trees that are up to 5% longer than the shortest trees (command **jump 50;**) was performed to help the swapper move between multiple local optima ('islands' *sensu* Maddison 1991). Finally, trees found with this command were again swapped with TBR, using the command **max*;** to retain only optimal trees.

Despite the fact that not all characters in a data matrix provide equally reliable evidence for phylogenetic inference, the philosophical justification for differential weighting—the logical derivation of this manifest lack of uniformity in the phylogenetic content of characters—remains contentious. Detractors maintain that differential weighting increases the background knowledge of a phylogenetic hypothesis and thus reduces its empirical content (Kluge 1989, 1997*b*; Siebert 1992; Brower 1999, 2000; Frost *et al.* 2001), while supporters differ radically in their opinions on the choice of weighting schemes (Farris 1969; Penny and Hendy 1985, 1986; Neff 1986; Wheeler 1986; Wheeler and Honeycutt 1988; Sharkey 1989; Williams and Fitch 1989; Wheeler 1990; Goloboff 1993; Knight and Mindell 1993; Simon *et al.* 1994). Over and above these opposing viewpoints is the proposition that differential weighting could be regarded as a method for exploring the sensitivity of the data to perturbation and, in combination with an appropriate optimality criterion, might thus provide a means of choosing among alternative hypotheses (Farris 1969; Carpenter 1988, 1994; Wheeler 1995; Scharff and Coddington 1997; Prendini 2000*a*; Arnedo *et al.* 2002).

Several authors (e.g. Wheeler 1995; Whiting *et al.* 1997; Zrzavý *et al.* 1998*a*, 2001; Edgecombe *et al.* 1999, 2000; Giribet and Wheeler 1999; Giribet and Ribera 2000; Giribet *et al.* 2000; Prendini 2000*a*) have suggested that, because phylogenetic results depend on the analytical assumptions, analyses should examine the effect of parameter variation (including differential weighting schemes) on results: 'sensitivity analysis' *sensu* Wheeler (1995). For example, higher homoplasy rates for transitions, as well as for third-codon positions in protein-coding genes, are well known (e.g. Brown *et al.* 1982; Cummings *et al.* 1995; Philippe *et al.* 1996; Yoder *et al.* 1996; Mitchell *et al.* 1997; Hassanin *et al.* 1998; Edgecombe *et al.* 2000; Simmons 2000; Wahlberg and Zimmermann 2000; and the present study is no exception), prompting many authors to advocate downweighting to decrease the putatively negative effects of this homoplasy (e.g. Miyamoto and Boyle 1989; Swofford and Olsen 1990; Meyer 1994; Mindell *et al.* 1996; Swofford *et al.* 1996; but see Björklund 1999; Källersjö *et al.* 1999; Wenzel and Siddall 1999; Simmons 2000). However, the choice of any particular weighting scheme (or parameter set) is arbitrary, hence the exploration of multiple parameters has been advocated as a means for discerning between robust relationships, which appear under a wide range of parameters, and unstable relationships, which appear only under particular parameters (Whiting *et al.* 1997; Zrzavý *et al.* 1998*a*, 2001; Edgecombe *et al.* 1999; Giribet and Wheeler 1999; Giribet and Ribera 2000; Giribet *et al.* 2000, 2002; Phillips *et al.* 2000; Prendini 2000*a*). The sensitivity of phylogenetic results to variation in the analytical parameters for molecular data—primarily the indel or gap : cost ratio and the transversion : transition or change ratio—has been widely explored (e.g. Wheeler 1995; Whiting *et al.* 1997; Wheeler and Hayashi 1998; Zrzavý *et al.* 1998*a*, 2001; Edgecombe *et al.* 1999, 2000; Giribet and Ribera 2000; Giribet *et al.* 2000, 2001*b*; Wheeler *et al.* 2001). Fewer studies have examined the sensitivity of morphological data, analysed separately (Prendini 2000*a*, 2001*c*) or in combination with molecular data (Whiting *et al.* 1997; Wheeler and Hayashi 1998; Zrzavý *et al.* 1998*a*, 2001; Edgecombe *et al.* 1999), to different analytical parameters, despite the fact that it would be logically inconsistent not to do so (Wheeler and Hayashi 1998).

The following parameters were varied in the present investigation. First, the effect of treating indels as missing data (effectively weighting to zero) was explored, following Whiting *et al.* (1997) and Giribet *et al.* (1999*a*, 1999*b*), to examine the conventional wisdom that gaps should be disregarded for phylogenetic analysis (e.g. Swofford and Olsen 1990; Williams 1992; Swofford *et al.* 1996; Yang and Rannala 1997). These analyses of the aligned sequence data were conducted separately and simultaneously with the morphological data, using NONA, according to the abovementioned commands.

Besides treating indels as missing, the indel or gap : cost ratio, the transversion : transition (tv : ts) or change ratio, and the relative weight of morphology were varied and analysed simultaneously and separately by direct optimisation, following previous authors (e.g. Wheeler 1995; Whiting *et al.* 1997; Wheeler and Hayashi 1998; Edgecombe *et al.*

1999; Giribet and Ribera 2000; Wheeler *et al.* 2001). Higher homoplasy rates for transitions are well known (e.g. Philippe *et al.* 1996; Yoder *et al.* 1996) and many authors have advocated downweighting to decrease putatively negative effects of this homoplasy (but see Wenzel and Siddall 1999).

In the direct optimisation analyses, as in similar studies using that method (e.g. Wheeler and Hayashi 1998; Edgecombe *et al.* 1999; Giribet and Ribera 2000), the indel cost represented the relative cost of the insertion or deletion of a base *versus* a base substitution, while the tv:ts cost represented the relative cost of a transversion *versus* a transition. Thus, if an indel ratio of 2:1 was specified, two base substitutions would equal a single indel, whereas if a tv:ts ratio of 4:1 was specified, four transitions would equal a single transversion. When the tv:ts ratio was set at a value other than unity, the indel cost was set according to the cost of transversions. The relative indel cost was varied from equal to base substitutions to twice and four times as costly (the 2:1 weighting approximates the gap:change ratio used during alignment). The tv:ts cost was similarly specified and, in addition, a transversion-only scheme (transition cost of zero) was employed, following Wheeler and Hayashi (1998), Edgecombe *et al.* (1999), Wheeler *et al.* (2001) and Giribet *et al.* (2002). In total, 12 combinations of indel and tv:ts costs were employed (with indel ratios of 1, 2, 4 and tv:ts ratios of 1, 2, 4, ∞). Following Giribet and Ribera (2000) and Giribet *et al.* (2002), the parameters are named 110, 111, 121, 141, 210, 211, 221, 241, 410, 411, 421, 441 (Table 7). According to this notation, parameter set 221 (gap:tv:ts) means that the indel (gap) cost is set twice the highest tv:ts (change) cost, in this case the tv, which is twice the ts cost, hence the ratio 221 implies costs for gap, tv and ts of 4, 2 and 1, respectively. In studies of the higher phylogeny of Arthropoda, optimal parameter sets have been experimentally found to be for gap:tv:ts = 211, 411, 221 (Wheeler 1995, 1997, 1998*a*; Wheeler and Hayashi 1998; Edgecombe *et al.* 1999; Wheeler *et al.* 2001) whereas for lower-level relationships, higher gap costs have been found to be optimal (Giribet and Wheeler 1999).

While the indel and tv:ts ratios were varied, the morphological data were assigned weights relative to the molecular data, in order to investigate the putative 'swamping' effect by relatively more abundant molecular characters (Miyamoto 1985; Swofford 1991). In this study, molecular characters were 4.5 times as numerous. In one group of analyses, morphological characters were weighted equal to the highest of the molecular costs (indels), as in Wheeler and Hayashi (1998), Giribet and Wheeler (1999*b*), Edgecombe *et al.* (1999) and Wheeler *et al.* (2001). In a separate group of analyses, morphological data were weighted equal to the base change cost, following Wheeler and Hayashi (1998). This resulted in 20 simultaneous analyses, in addition to the 12 separate analyses of the molecular data in which indel and tv:ts ratios were varied.

All analyses in which indel ratio, tv:ts ratio, and relative weight of morphology were varied and subjected to direct optimisation, were performed using batch files spawning the program POY Ver. 2.0 (Gladstein and Wheeler 1996–2000) in a cluster of 564 500–1000-MHz processors connected in parallel with PVM software (see Janies and Wheeler 2001). Stepmatrices were invoked with the command **–molecularmatrix**, with an argument for the relevant stepmatrix, for example **–molecularmatrix 221**, and morphological weights were assigned with the command **–weight N**. The following commands were used for the search (Gladstein and Wheeler 1996–2000; Giribet and Ribera 2000):

–parallel: executes in parallel using PVM.
–solospawn 5: sets five slave jobs to be spawned in PVM.
–noleading: does not count leading and trailing gaps.
–norandomizeoutgroup: prevents randomisation of the outgroup in **–random** and **–multibuild**.
–seed –1: sets seed for pseudo-random number generation, using system time, in seconds (**–1**).
–maxtrees 20: holds 20 trees in memory.
–random 10: performs 10 random addition sequences (build through swapping); since the option **–norandomizeoutgroup** is specified, the outgroup is unaffected.
–fitchtrees: saves the most diverse cladograms that can be found for each island.
–ratchettbr 20: performs 10 iterations of the parsimony ratchet (Nixon 1999*b*), using TBR branch swapping.
–ratchetpercent 50: reweights 50% of the characters at each iteration.
–ratchetseverity 2: reweights the characters by a factor of two.
–ratchettrees 2: holds two starting trees in memory at each iteration.
–multibuild 10: performs 10 random addition sequence builds (no swapping), of which the best are submitted to branch swapping.

Table 7. Molecular stepmatrices used in sensitivity analyses with POY (Gladstein and Wheeler 1997)

Gap:change	tv:ts			
	∞	1	2	4
1	110:	111:	121:	141:
	0 1 0 1 1	0 1 1 1 1	0 2 1 2 2	0 4 1 4 4
	1 0 1 0 1	1 0 1 1 1	2 0 2 1 2	4 0 4 1 4
	0 1 0 1 1	1 1 0 1 1	1 2 0 2 2	1 4 0 4 4
	1 0 1 0 1	1 1 1 0 1	2 1 2 0 2	4 1 4 0 4
	1 1 1 1 0	1 1 1 1 0	2 2 2 2 0	4 4 4 4 0
2	210:	211:	221:	241:
	0 1 0 1 2	0 1 1 1 2	0 2 1 2 4	0 4 1 4 8
	1 0 1 0 2	1 0 1 1 2	2 0 2 1 4	4 0 4 1 8
	0 1 0 1 2	1 1 0 1 2	1 2 0 2 4	1 4 0 4 8
	1 0 1 0 2	1 1 1 0 2	2 1 2 0 4	4 1 4 0 8
	2 2 2 2 0	2 2 2 2 0	4 4 4 4 0	8 8 8 8 0
4	410:	411:	421:	441:
	0 1 0 1 4	0 1 1 1 4	0 2 1 2 8	0 4 1 4 16
	1 0 1 0 4	1 0 1 1 4	2 0 2 1 8	4 0 4 1 16
	0 1 0 1 4	1 1 0 1 4	1 2 0 2 8	1 4 0 4 16
	1 0 1 0 4	1 1 1 0 4	2 1 2 0 8	4 1 4 0 16
	4 4 4 4 0	4 4 4 4 0	8 8 8 8 0	16 16 16 16 0

–slop 5 –checkslop 10: checks all cladogram lengths that are within 0.5% and 1% of the current minimum value; this option slows down the search but is less affected by the heuristics of tree calculation shortcuts (Edgecombe *et al.* 1999; Giribet and Ribera 2000).

The complete command sequence for a simultaneous analysis under equal weighting (using stepmatrix 111 and morphology weighted 1), where the files 12S, 16S, 28S, COI and morph represent the various partitions and T111.tre represents the output file, is as follows: **poy –parallel –solospawn 5 –ratchettbr 20 –ratchetpercent 50 –ratchetseverity 2 –ratchettrees 2 –norandomizeoutgroup –noleading –molecularmatrix 111 –fitchtrees –maxtrees 20 –multibuild 10 –random 10 –seed –1 –slop 5 –checkslop 10 12S 16S 28S COI –weight 1 morph >T111.tre**.

The final component of the sensitivity analyses investigated the effects of *a posteriori* differential weighting on the aligned sequence data analysed separately and simultaneously with the morphological data. Two methods of analysis that allow the total suite of characters to determine the weights of individual characters were employed: successive approximations weighting (Farris 1969) and implied weighting (Goloboff 1993, 1995). Successive weighting, using the consistency index (*CI*) as a weighting function (Goloboff 1991), was implemented with NONA, by invoking the swt.run file (command sequence: **run swt.run hold10000; hold/10; mult*100; jump50; max*;**). Successive weighting has been criticised for various reasons: (*1*) the search may become trapped in a local optimum that depends on the starting tree (Neff 1986; Swofford *et al.* 1996); (*2*) use of the *CI* or the rescaled *CI* (consistency index × retention index) as weighting function is problematic because it does not always increase with less homoplasy (Goloboff 1991; Siebert 1992); (*3*) the tree(s) resulting from the successive weighting procedure are not always among the set of trees derived from the initial analysis with equal weighting, and in some data sets with low *CI*, successive weighting yields more trees than the initial search (Siebert 1992); (*4*) there is no objective criterion for comparing trees, that is, if a tree is found to be optimal, one cannot say how much worse an alternative tree is (Goloboff 1993; Swofford *et al.* 1996).

Unlike successive weighting, implied weighting allows simultaneous character weighting and tree search, thus avoiding the pitfalls of iterative searches for preliminary trees, and provides an optimality criterion (maximum fit) for tree selection (Goloboff 1993; Arnedo *et al.* 2002). The primary drawback of the current implementation of this method is the existence, in the function relating homoplasy and character weight, of a concavity constant, *k*, the value of which must be arbitrarily assigned (Turner and Zandee 1995; Prendini 2000*a*; Arnedo *et al.* 2002). Increasing the *k* value produces a progressively weaker weighting function, such that higher *k* values are expected to yield results approaching those obtained by analysis with equal weighting (low *k* values yield results approaching those obtained by clique analysis).

Pee-Wee Ver. 2.6 (Goloboff 1997*b*) was used for analyses with implied weighting, according to the following command sequence: **hold10000; hold/10; mult*100; jump50; max*;**. Gladstein and Wheeler (1996–2000) noted that, because molecular data usually exhibit a greater number of changes, the currently implemented weighting function, which is proportional to the inverse of the number of extra steps, might tend to favour morphological characters over molecular ones, a problem that, according to Arnedo *et al.* (2002), could be circumvented by using the mildest *k* value ($k = 6$). In view of the fact that there is currently no philosophical justification for the choice of any particular *k* value, the present analyses with implied weighting made use of six values for *k*, spanning the input range permitted by Pee-Wee (specified with command **conc N;**). As in the analyses with equal weighting, all characters were weighted equally *a priori* and indels were treated as a fifth character state. In addition, a separate, identical group of analyses was conducted in which indels were treated as missing data.

Note that the use of alternative methods of parsimony analysis (e.g. equal *vs* implied weighting) in the present context is not regarded as syncretistic, in the sense discussed above with reference to the use of parsimony, distance-based and statistical methods of phylogenetic analysis. Although the various procedures used here may differ in optimality criterion (e.g. minimum length *vs* maximum fit), they correspond in their use of synapomorphy (cf. overall similarity or distance) as the primary source of evidence and in their application of parsimony (cf. likelihood) as the decisive principle. Furthermore, trees obtained by alternative methods of parsimony analysis can be compared directly in terms of length, fit, *CI* and retention index (*RI*) (these indices merely reflecting the method and intensity of weighting used), whereas a comparison of indices obtained by parsimony, distance-based and statistical methods would be impossible and, in any case, meaningless.

Considering all the analyses mentioned above, the three values used for the indel cost (1, 2, 4), four values for the tv : ts ratio (1, 2, 4, ∞) and two values used for the morphology (gap, change) resulted in 20 parameter combinations, and the use of equal, successive and implied weighting, with indels treated as missing or as a fifth state resulted in a further 16 parameter combinations. These combinations sum to a total of 36 sets of assumptions, each of which was applied to the molecular data analysed separately and simultaneously with the morphological data. As in other studies (e.g. Wheeler 1995; Whiting *et al.* 1997; Prendini 2000*b*; Wheeler *et al.* 2001), results of the sensitivity analyses are summarised by means of 50% majority rule (Margush and McMorris 1981), or 50% compromise (*sensu* Nixon and Carpenter 1996*b*), and strict consensus trees. The problems of using majority-rule consensus trees as a means of resolving ambiguous strict consensus trees have been well elaborated by Nixon and Carpenter (1996*b*) and Sharkey and Leathers (2001), among others. Their use in the present context is justified on the grounds that they serve a different purpose. Here, majority-rule consensus trees are presented, alongside strict consensus trees, to provide a graphical representation of the results of the sensitivity analyses. Nodes that appear in the majority-rule trees but are collapsed in the strict consensus trees were obtained under the majority of weighting regimes, hence more confidence may be placed in the supposition that they are robustly supported by the data than in the alternatives, which were retrieved only under specific weighting regimes.

Again following previous authors (Wheeler 1995; Wheeler and Hayashi 1998; Edgecombe *et al.* 1999, 2000; Giribet and Ribera 2000; Giribet *et al.* 2000, 2001*b*; Wheeler *et al.* 2001), congruence between morphological and molecular data partitions was used as an optimality criterion to select the optimal (most corroborated) tree—that which minimises character conflict among the data—from among the various alternatives analysed under equal or *a priori* differential weighting. This is an extension of parsimony for, just as the aim of parsimony analysis is to locate the tree that minimises the number of steps, the aim of sensitivity analysis is to determine the parameter set that minimises incongruence among the data (Wheeler 1995; Edgecombe *et al.* 1999). Incongruence among data partitions was measured by the ILD (Mickevich and Farris 1981; Farris *et al.* 1994), calculated by dividing the difference between the overall tree length and the sum of its data partitions:

$$\mathrm{ILD} = (\mathrm{LENGTH}_{\mathrm{combined}} - \Sigma\mathrm{LENGTH}_{\mathrm{partitioned}})/\mathrm{LENGTH}_{\mathrm{combined}}$$

The relative degree of support for branches in the optimal trees was assessed with branch support or decay indices (Bremer 1988, 1994; Donoghue *et al.* 1992). Branch support indices up to 60 extra steps (setting the maximum number of trees held in memory to 10000) were calculated with NONA, by means of the following command sequence:

h10000; bsupport 60;. As there were more than 10000 trees up to 60 extra steps, obtaining accurate branch support values required 60 successive searches to be conducted, starting by searching for trees only one step longer than the shortest, and continuing with searches for progressively longer trees until values had been obtained for nodes with the greatest support. Branch supports were calculated in POY by invoking the **–bremer** command. Cladograms were prepared using WinClada, Ver. 0.9.9+ (Nixon 1999*a*). Tree length, fit, consistency and retention indices were calculated using phylogenetically informative characters only (Bryant 1995).

Results

Sequence data analysis

The alignment length of each of the four fragments, across the 15 terminal taxa for which sequence data were obtained, is provided in Table 8. The aligned 12S rDNA sequences that gave the shortest tree (in MALIGN) comprised 343 sites, 18 (5%) of which contained at least one gap in one sequence. The aligned 16S rDNA sequences that gave the shortest tree comprised 489 sites, 14 (3%) of which contained at least one gap in one sequence. As expected, most indels in the 12S rDNA and 16S rDNA sequences were restricted to putative loop areas of the rDNA molecules, whereas the regions between contained fewer indels.

The aligned 12S rDNA sequences comprised 181 constant sites and 162 variable sites (including gaps), 127 of which were informative, whereas the aligned 16S rDNA sequences comprised 262 constant sites and 227 variable sites (including gaps), 166 of which were informative (Table 8 provides counts with gaps excluded). The frequencies of variable and informative sites (including gaps) in the 12S rDNA alignment (47 and 37%, respectively) were slightly greater than those in the 16S rDNA alignment (46 and 34%, respectively), despite the fact that the 12S rDNA alignment was 30% shorter. This suggests that the 12S rDNA fragment is less conserved, contrary to conventional wisdom (e.g. Ballard *et al.* 1992). As is typical of arthropod mtDNA (DeSalle *et al.* 1987; Simon *et al.* 1994; Wahlberg and Zimmermann 2000), the 12S rDNA and 16S rDNA sequences were AT-rich: overall average incidence in 12S rDNA of A = 40%, C = 10%, G = 17% and T = 34%; overall average incidence in 16S rDNA of A = 33%, C = 13%, G = 18% and T = 36% (Table 9).

The 658-bp *COI* sequence alignment, corresponding to 219 codons, contained 432 constant sites and 226 variable sites, 167 of which were informative (Table 8). As expected, the frequencies of variable and informative sites in the *COI* alignment (34 and 25%, respectively) were considerably lower than those in the 12S rDNA and 16S rDNA alignments. Also typical for protein-coding genes (Philippe *et al.* 1996; Yoder *et al.* 1996; Edgecombe *et al.* 2000; Wahlberg and Zimmermann 2000), most of the variation was in the third codon position: 136 of 175 variable third positions were informative, compared with 27 of 43 variable first positions and a mere 4 of 8 variable second positions. The frequencies of informative sites in the first, second and third positions (16, 2 and 81%, respectively) compare favourably with those obtained for a homologous fragment of *COI* (amplified with the same primers) in nymphalid butterflies by Wahlberg and Zimmermann (2000): 16, 3 and 80%. As with the 12S rDNA and 16S rDNA, the *COI* sequences were AT-rich, especially at the third codon position (DeSalle *et al.* 1987; Simon *et al.* 1994; Wahlberg and Zimmermann 2000): overall average incidence of A = 20%, C = 13%, G = 24% and T = 43%; average incidence at third position of A = 20%, C = 1%, G = 23%, and T = 56% (Table 9). These nucleotide frequencies compare favourably with those provided by Wahlberg and Zimmermann (2000) for nymphalid butterflies: overall average incidence of A = 32%, C = 15%, G = 14%, and T = 39%; average incidence at third position of A = 45%, C = 7%, G = 1%, and T = 47%.

In comparison with the fragments obtained from the mitochondrial genome, the D3 region of the nuclear 28S rDNA gene was considerably more conserved. The 312-bp sequence alignment contained 283 constant sites and 29 variable sites, only 11 of which were informative, hence the frequencies of variable and informative sites were only 9 and 4%, respectively (Table 8). This conforms to similar

Table 8. Distribution of constant, variable and phylogenetically informative positions in aligned sequences of four gene loci (28S rDNA, 12S rDNA, 16S rDNA and *COI*) among exemplar species of the scorpionid genera, *Heterometrus*, *Opistophthalmus*, *Pandinus* and *Scorpio*, and the diplocentrid genus *Nebo*

In each case, the number of positions precedes the percentage frequency (in parentheses). '+ gaps' denotes counts in which gaps (in the 12S rDNA and 16S rDNA alignments) were included

Genome:	Nuclear			Mitochondrial				Total
Function:		Ribosomal			Protein-coding			
Gene locus:	28S rDNA	12S rDNA	16S rDNA	*COI*	1st	2nd	3rd	
Length	312	343	489	658				1802
Constant	283 (91)	181 (53)	262 (54)	432 (66)	176 (41)	211 (49)	45 (10)	1158 (64)
Variable	29 (9)	158 (46)	226 (46)	226 (34)	43 (19)	8 (4)	175 (77)	639 (35)
Variable + gaps		162 (47)	227 (46)					651 (36)
Informative	11 (4)	123 (36)	163 (33)	167 (25)	27 (16)	4 (2)	136 (81)	464 (26)
Informative + gaps		127 (37)	166 (34)					471 (26)

frequencies of variable and informative sites obtained in a study of Opiliones phylogeny (Giribet *et al.* 1999*a*) based on a homologous fragment of 28S rDNA (amplified with the same primers): 18 and 10%, respectively. The values obtained by Giribet *et al.* (1999*a*) are predictably higher given the deeper phylogenetic level focused on in that study (families as opposed to genera). The correspondingly higher proportion of CG nucleotides in the nuclear genome, compared with the mitochondrial genome, was also confirmed by the 28S rDNA sequences: overall average incidence of A = 22%, C = 27%, G = 35%, and T = 17% (Table 9).

The combined alignment of the four fragments comprised 1802 sites, of which 1158 were constant and 651 were variable (Table 8). Only 32 (3%) of the sites contained at least one gap. Including gaps, 471 sites, or slightly more than one quarter of the combined alignment length, were informative. The estimated transversion/transition ratio for combined data was 0.74 (Table 9). Most of the changes comprised A↔G transitions, A↔T transversions and C↔T transitions, which predominated in the mitochondrial data. Although fairly numerous in the protein-coding locus, G↔T transitions were less common in the ribosomal loci.

Separate analysis of the morphological data

Separate analysis of the 101 informative morphological characters with equal, successive and implied weighting under six *k* values located a single most parsimonious tree (MPT) in all cases except with implied weighting under $k = 3$, where two MPTs were obtained. The length, fit, *CI* and *RI* of the MPTs is presented in Table 10.

As observed in other analyses based on morphological data (Prendini 2000*a*, 2001*c*), the length of the MPTs increased predictably in proportion to the severity of the weighting and the fittest MPTs were obtained in the analyses with implied weighting under moderate to mild concavity ($k = 3$–6). However, only MPTs obtained by analyses with $k > 3$ were fitter (2–4%) than those obtained by the analyses with equal weighting or successive weighting, whereas MPTs obtained by analyses with values of $k < 3$ were less fit (4–9%). For example, the MPT obtained by analysis with $k = 1$ was three steps longer and 9% less fit than that obtained with equal weighting, whereas the MPT obtained by analysis with $k = 6$ was the same length as, but 4% fitter than, that obtained with equal weighting.

Although differing substantially in length and fit, the MPTs were fairly similar topologically (among the analyses with implied weighting, identical topologies were obtained under $k = 1$–2 and under $k = 4$–6), as indicated by the majority rule (>50%), or 50% compromise (*sensu* Nixon and Carpenter 1996*b*), and strict consensus trees (Fig. 4). All except two nodes, which collapsed in the strict consensus tree (Fig. 4*A*), were obtained by the eight analyses under vastly different weighting regimes and may thus be regarded as robustly supported by the morphological data. The two nodes that appear in the majority-rule tree (Fig. 4*B*) but are collapsed in the strict consensus tree were obtained under the majority of weighting regimes, hence more confidence may be placed in the supposition that they are robustly supported by the morphological data than in the alternatives, which were retrieved only under specific weighting regimes.

All analyses, regardless of weighting scheme, retrieved the following arrangement of genera (Fig. 4*A*): (*Opistophthalmus* (*Scorpio* (*Heterometrus* + *Pandinus*))). Only the relative placements of three species of

Table 9. Frequencies of nucleotides, transitions and transversions in sequences of four gene loci (28S rDNA, 12S rDNA, 16S rDNA and *COI*) among exemplar species of the scorpionid genera, *Heterometrus*, *Opistophthalmus*, *Pandinus* and *Scorpio*, and the diplocentrid genus *Nebo*

All frequencies are averages (rounded) over all taxa

Genome:	Nuclear			Mitochondrial				Total
Function:	Ribosomal			Protein-coding				
Gene locus:	28S rDNA	12S rDNA	16S rDNA	*COI*	1st	2nd	3rd	
Nucleotides								
A	22	40	33	20	28	13	20	29
C	27	10	13	13	13	25	1	16
G	35	17	18	24	30	18	23	24
T	17	34	36	43	30	44	56	33
Transitions (ts)								
AG	1	18	28	36	5	0	30	21
CT	4	10	18	11	5	1	5	11
Transversions (tv)								
AC	1	3	4	1	1	0	0	2
AT	1	23	26	23	2	0	21	18
CG	0	1	1	1	0	0	0	1
GT	1	6	7	21	1	0	20	9
tv:ts	0.42	1.11	0.83	1.0	0.37	0.37	1.11	0.74

Opistophthalmus and two species of *Pandinus* differed. Analyses with equal weighting, successive weighting and implied weighting under k = 4–6 placed *O. holmi* basal to a group comprising *O. capensis* and *O. carinatus*, whereas analyses with implied weighting under k = 1–3 placed *O. carinatus* basal to a group comprising *O. capensis* and *O. holmi*. Analyses with equal weighting and implied weighting under k = 4–6 placed *P. dictator* and *P. imperator* as the monophyletic sister-group of the (*P. cavimanus* + *P. viatoris*) group, whereas analyses with successive weighting and implied weighting under k = 1–2 placed *P. dictator* and *P. imperator* in a pectinate arrangement, basal to the (*P. cavimanus* + *P. viatoris*) group. The two MPTs retrieved in the analysis with implied weighting under k = 3

Table 10. Summary of statistical differences among the most parsimonious trees (MPTs) obtained by separate and simultaneous analysis of the morphological and aligned molecular data (gaps included or excluded) under equal weights (EW), successive weights (SW) and implied weights (IW) with six values for the concavity constant (k), arranged in order of increasing fitness (F_i)
Unweighted length is reported for the SW trees

Analysis	MPTs	Steps	Fit (F_i)	Fit (%)	*CI*	*RI*
Morphology						
IW, k = 1	1	254	601.7	44	55	65
IW, k = 2	1	254	715.2	49	55	65
EW	1	251	780.4	53	56	66
SW	1	252	780.4	53	55	65
IW, k = 3	2	254	781	53	55	65
IW, k = 4	1	251	820.1	55	56	66
IW, k = 5	1	251	847.7	56	56	66
IW, k = 6	1	251	868	57	56	66
Molecular – gaps						
IW, k = 1	1	1755	2251.2	29	48	47
IW, k = 2	1	1744	2835.5	33	48	48
EW	1	1740	3185.3	36	48	48
SW	1	1740	3185.3	36	48	48
IW, k = 3	1	1744	3191.4	36	48	48
IW, k = 4	1	1744	3418.1	38	48	48
IW, k = 5	1	1744	3577.4	39	48	48
IW, k = 6	1	1744	3701.5	40	48	48
Molecular + gaps						
IW, k = 1	1	1787	2312.9	29	49	48
IW, k = 2	1	1787	2909.2	34	49	48
EW	4	1785	2555.1	26	49	48
SW	1	1785	3268.2	36	49	48
IW, k = 3	1	1787	3269.8	37	49	48
IW, k = 4	1	1787	3499.5	38	49	48
IW, k = 5	1	1787	3661.4	39	49	48
IW, k = 6	1	1787	3787.8	40	49	48
Simultaneous – gaps						
IW, k = 1	1	1998	2843.7	31	49	51
IW, k = 2	1	1998	3547.2	36	49	51
EW	1	1997	3968.1	39	49	51
SW	1	1997	3968.1	39	49	51
IW, k = 3	1	1998	3969.6	39	49	51
IW, k = 4	1	1998	4236.2	41	49	51
IW, k = 5	1	1998	4422.4	42	49	51
IW, k = 6	1	1998	4567.4	43	49	51
Simultaneous + gaps						
IW, k = 1	1	2043	2897.8	31	50	51
IW, k = 2	1	2043	3614.2	36	50	51
EW	2	2043	4042.1	39	50	51
SW	1	2043	4044.1	39	50	51
IW, k = 3	1	2043	4044.1	39	50	51
IW, k = 4	1	2043	4315.1	41	50	51
IW, k = 5	1	2043	4504.3	42	50	51
IW, k = 6	1	2043	4651.5	43	50	51

differed solely with respect to the positions of *P. dictator* and *P. imperator*, as described above.

The MPT retrieved by the analysis with implied weighting under $k = 6$ is both shortest and fittest, and may be regarded as the optimal tree obtained by separate analysis of the morphological data. This topology was obtained by analysis with equal weighting and implied weighting under $k = 4$–5, and is also identical to the majority-rule consensus tree (Fig. 4*B*).

Separate analysis of the molecular data

Separate analysis of the aligned molecular data under the eight weighting regimes, with gaps (indels) included or excluded, yielded 16 different results (Table 10). A single MPT was located in all analyses except with equal weighting and gaps included, when four MPTs were retrieved. The *CI*, *RI* and rescaled fitness (per cent) values were in all cases lower than those for the corresponding analyses in which the morphological data were analysed separately.

Trends in tree length and fitness were otherwise similar to those observed among the separate morphological analyses. MPTs obtained from the analyses with differential weighting were mostly longer than those from the analyses with equal weighting. MPTs obtained by the analyses with implied weighting under moderate to mild concavity ($k = 3$–6) were fitter than those obtained with successive weighting and equal weighting, which were, in turn, fitter than those obtained with implied weighting under strong concavity ($k = 1$–2). A single exception concerns the analysis with equal weighting and gaps included, which achieved the lowest fitness. Besides this, and a slight increase in fitness in the analyses with implied weighting under $k = 2$–3, there were few differences between the analyses in which gaps were excluded and those in which gaps were included, an observation that may be attributed to the small number of gaps. However, the MPTs retrieved by analyses in which gaps were included demonstrated a greater *CI*, providing empirical support for arguments that gaps should be included in phylogenetic analysis (Giribet and Wheeler 1999*b*; Gatesy and Arctander 2000; Simmons 2000; Simmons and Ochoterena 2000).

Compared with the strict and majority-rule consensus trees obtained by separate analyses of the morphological data (Fig. 4), the corresponding consensus trees for the aligned molecular data (Fig. 5*A*, *B*) reflect less topological concordance and hence greater parameter sensitivity of the molecular data set, despite the fact that it is 77% larger (based on the number of phylogenetically informative sites). Nonetheless, all except five nodes, which collapsed in the strict consensus tree (Fig. 5*A*), were obtained by the 16 analyses and may thus be regarded as robustly supported by the aligned molecular data. None of these nodes is incompatible with the MPTs retrieved by separate analyses of the morphological data. Significantly, the monophyly of all four scorpionid genera is supported.

The five nodes that appear in the majority-rule consensus tree (Fig. 5*B*) but are collapsed in the strict consensus tree were obtained in more than 50% of the analyses based on fixed alignment. Two of these nodes reflect groups that were obtained in all or the majority of separate analyses of the morphological data: the (*Heterometrus* + *Pandinus*) group and the (*P. dictator* + *P. imperator*) group, respectively. The other three nodes are incompatible with the MPTs retrieved by separate analyses of the morphological data. Two of the latter concern internal rearrangements within *Opisthophthalmus*, whereas the third reflects the relative positions of *Opistophthalmus* and *Scorpio*, as follows: (*Scorpio* (*Opistophthalmus* (*Heterometrus* + *Pandinus*))).

Separate analyses of the molecular data by direct optimisation, with 12 combinations of indel and tv:ts costs, revealed similarly less topological concordance and greater

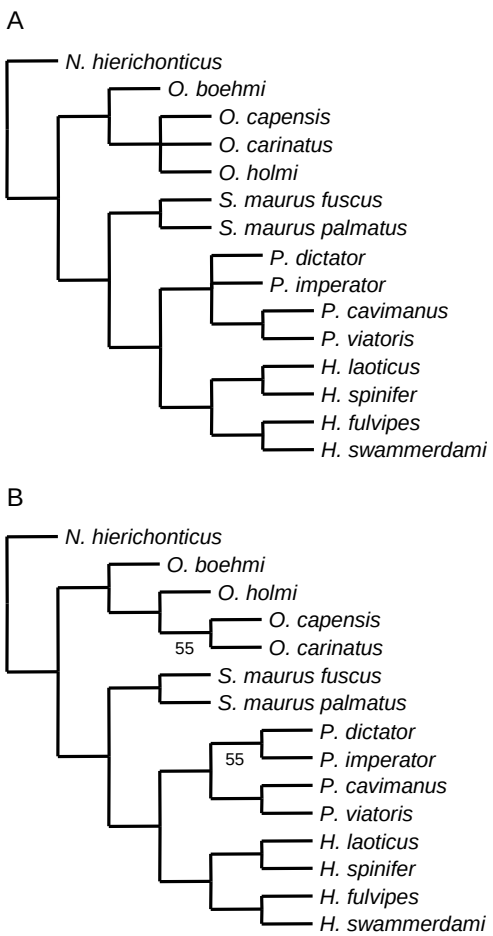

Fig. 4. Consensus of the MPTs obtained by eight separate analyses of the morphological data (Table 3) in which weighting regime was varied (Table 10). *A*, Strict consensus. *B*, Majority rule (>50%) consensus. The frequencies with which nodes were retrieved in >50% of the analyses are indicated below the branches for frequencies of >50% but <100%. Remaining uncollapsed nodes were retrieved in all analyses.

parameter sensitivity than separate analyses of the morphological data set (Fig. 5*C*, *D*). Only four nodes appearing in the strict consensus tree (Fig. 5*C*) were obtained by all 12 analyses and may be regarded as robustly supported by the optimised molecular data. However, three of these nodes support the monophyly of scorpionid genera (*Heterometrus* monophyly is not supported in all direct optimisation analyses).

Seven nodes that appear in the majority-rule consensus tree (Fig. 5*D*) but are collapsed in the strict consensus tree were obtained in more than 50% of the analyses based on direct optimisation. Four of these nodes reflect groups that were obtained in at least one separate analysis of the morphological data: (*Heterometrus*); (*H. laoticus* + *H. spinifer*); and (*P. imperator* (*P. cavimanus* + *P. viatoris*)). The three nodes that are incompatible concern internal rearrangements within *Opistophthalmus* and the relative positions of *Opistophthalmus* and *Scorpio*, which differ as follows: (*Scorpio* (*Heterometrus* (*Opistophthalmus* + *Pandinus*))). The placement of *Scorpio* obtained in the majority of analyses with direct optimisation (Fig. 5*D*) was also obtained in the majority of analyses based on fixed alignment (Fig. 5*B*), whereas the placement of *Opistophthalmus* obtained in the majority of analyses with direct optimisation was retrieved in only a single analysis of the aligned data (equal weighting with gaps included).

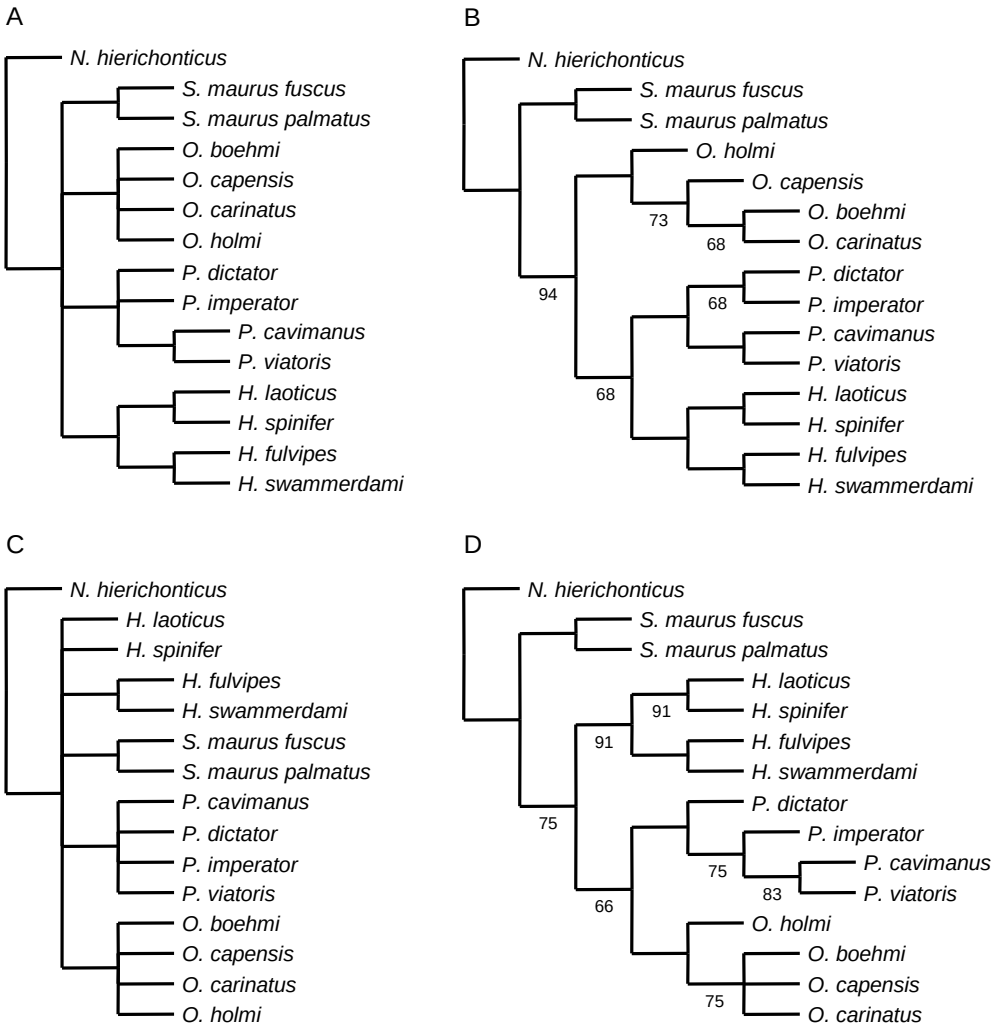

Fig. 5. *A*, *B*, Consensus of the MPTs obtained by 16 separate analyses of the aligned molecular data (Accessory Material) in which weighting regime was varied and gaps were included or excluded (Table 10). *C*, *D*, Consensus of the MPTs obtained by 12 separate analyses of the optimised molecular data in which indel (gap) cost and tv : ts ratio were varied (Tables 7, 11). *A*, *C*, Strict consensus. *B*, *D*, Majority rule (>50%) consensus. The frequencies with which nodes were retrieved in >50% of the analyses are indicated below the branches for frequencies of >50% but <100%. Nodes retrieved in <50% of the analyses are collapsed. Remaining uncollapsed nodes were retrieved in all analyses.

Simultaneous analysis of all the data

Sixteen different results were obtained by simultaneous analysis of the morphological and aligned molecular data under the eight weighting regimes, with gaps (indels) included or excluded (Table 10). A single MPT was retrieved in all cases except with equal weighting and gaps included, where two MPTs were obtained. As expected, the *CI*, *RI* and rescaled fitness (per cent) values were in all cases greater than those for the corresponding analyses in which the aligned molecular data were analysed separately.

Trends in tree fitness were again similar to those obtained among the separate analyses of the morphological and aligned molecular data. MPTs obtained by the analyses with implied weighting under moderate to mild concavity (k = 4–6) were fitter than those obtained with successive weighting and equal weighting, which were, in turn, fitter than those obtained with implied weighting under strong concavity (k = 1–2). When gaps were excluded, MPTs were longer in analyses with implied weighting than in analyses with equal weighting or successive weighting, but all MPTs were the same length when gaps were included. No difference in fitness was found between the MPTs obtained from the analyses in which gaps were included and those obtained from corresponding analyses in which gaps were excluded. However, the MPTs retrieved by analyses in which gaps were included again demonstrated a greater *CI*.

The results of simultaneous analysis were more stable, that is, less sensitive to parameter variation, than those for the corresponding analyses in which the aligned molecular data were analysed separately. As reflected in the consensus trees (Fig. 6*A*, *B*), all except one node, which collapsed in the strict consensus tree (Fig. 6*A*), were obtained by the 16 analyses under vastly different weighting regimes and may thus be regarded as robustly supported by all the data. Only the relative placements of two species of *Pandinus* differed among simultaneous analyses of the morphological and aligned molecular data. Analyses with successive weighting (gaps included) and implied weighting under k = 1–6 (gaps included or excluded) placed *P. dictator* and *P. imperator* as the monophyletic sister-group of the (*P. cavimanus* + *P. viatoris*) group, whereas analyses with equal weighting (gaps excluded) and successive weighting (gaps excluded) placed *P. dictator* and *P. imperator* in a pectinate arrangement, basal to the (*P. cavimanus* + *P. viatoris*) group. The two MPTs retrieved in the analysis with equal weighting (gaps included) differed solely with respect to the positions of *P. dictator* and *P. imperator*, as described above.

The consensus trees obtained by simultaneous analysis of the morphological and aligned molecular data (Fig. 6*A*, *B*) differ from those for the separately analysed morphological data (Fig. 4) only as regards the internal rearrangements within *Opistophthalmus*. The simultaneous analyses unanimously support the following arrangement, also retrieved by the separate morphological analyses with implied weighting under k = 1–3: (*O. carinatus* (*O. capensis* + *O. holmi*)). More importantly, the monophyly of all four scorpionid genera is supported by all the simultaneous analyses, as are their relative placements: (*Opistophthalmus* (*Scorpio* (*Heterometrus* + *Pandinus*))). The alternative arrangements of *Opistophthalmus* and *Scorpio*, retrieved by the majority of separate analyses of the aligned molecular data (Fig. 6*B*), are not supported by simultaneous analysis.

Simultaneous analyses of the morphological and molecular data by direct optimisation, with 12 combinations of indel and tv:ts costs, also revealed greater topological concordance and stability than separate analyses of the molecular data, and the resultant consensus trees compare favourably with those obtained by simultaneous analysis of the morphological and aligned molecular data (Fig. 6*C*, *D*). All except four nodes, which collapsed in the strict consensus tree (Fig. 6*C*), were obtained by the 12 analyses and may thus be regarded as robustly supported by all the data under direct optimisation. None of these nodes is incompatible with the MPTs retrieved by separate analyses of the morphological data or simultaneous analyses of the morphological and aligned molecular data. The monophyly of all four scorpionid genera is again unanimously supported as are their relative placements: (*Opistophthalmus* (*Scorpio* (*Heterometrus* + *Pandinus*))).

Three nodes that appear in the majority-rule consensus tree (Fig. 6*D*) but are collapsed in the strict consensus tree were obtained in more than 50% of the analyses based on direct optimisation. Two of these nodes reflect groups that were obtained in all separate analyses of the morphological data and all simultaneous analyses of the morphological and aligned molecular data: the group comprising *O. capensis*, *O. carinatus* and *O. holmi*; and the position of *Scorpio* as sister to the (*Heterometrus* + *Pandinus*) group. The third node reflects a group that was obtained in the majority of separate morphological analyses but is incompatible with all simultaneous analyses of the morphological and aligned molecular data: (*O. capensis* + *O. carinatus*). The relative placements of two *Pandinus* species, *P. dictator* and *P. imperator*, could not be resolved by the majority of simultaneous analyses with direct optimisation.

Among the simultaneous analyses of the morphological and aligned molecular data (gaps included), the MPT retrieved by the analysis with implied weighting under k = 6 is fittest, and may be regarded as the optimal tree based on fixed alignment (Fig. 7*A*). This topology was obtained by analysis with successive weighting (gaps included) and implied weighting under k = 1–5 (gaps included or excluded), and is also identical to the majority-rule consensus tree of the MPTs obtained by simultaneous analysis of the morphological and aligned molecular data (Fig. 6*B*).

The optimal tree obtained by simultaneous analysis of the morphological and molecular data with direct optimisation,

under the weighting regime that minimised topological incongruence among the data partitions (ILD = 0.0119), is provided in Fig. 7*B*. This MPT was obtained by analysis with a gap:tv:ts ratio of 211 (Table 7)—implying costs for indel (gap), tv and ts of 2, 1 and 1, respectively—and morphological data weighted equal to the tv:ts cost (Table 11). This optimal parameter set compares favourably with that found in other studies of arthropod phylogeny, where optimal parameter sets have been experimentally found to be for gap:tv:ts = 211, 411, 221 (Wheeler 1995, 1997, 1998*a*; Wheeler and Hayashi 1998; Edgecombe *et al.* 1999; Wheeler *et al.* 2001). Surprisingly, ILD values calculated for the simultaneous analyses based on fixed alignment (under equal weighting) were lower than the minimum ILD obtained by direct optimisation—0.0030 for the analysis with gaps excluded and 0.0034 for the analysis with gaps included—but these topologies are identical to the optimal tree obtained with direct optimisation (Fig. 7*B*).

The topologies shown in Fig. 7 are almost identical, differing only in the relative placements of *P. dictator* and *P. imperator*, and again confirm the monophyly of the four scorpionid genera, and their relative placements as follows: (*Opistophthalmus* (*Scorpio* (*Heterometrus* + *Pandinus*))). A summary of relationships among the four genera, with unambiguously optimised morphological synapomorphies indicated, and including the count of molecular

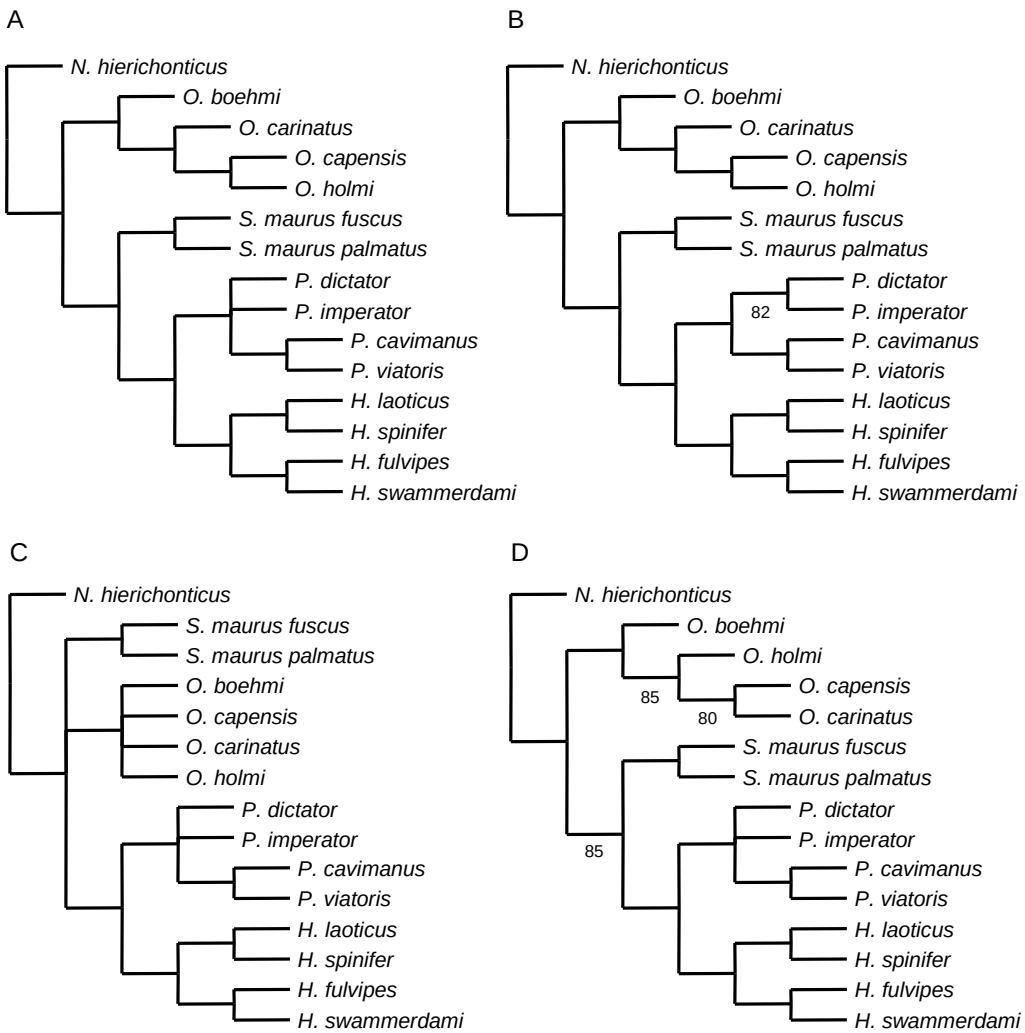

Fig. 6. *A*, *B*, Consensus of the MPTs obtained by 16 simultaneous analyses of the morphological data (Table 3) and aligned molecular data (Accessory Material) in which weighting regime was varied and gaps were included or excluded (Table 10). *C*, *D*, Consensus of the MPTs obtained by 20 simultaneous analyses of the morphological data (Table 3) and optimised molecular data in which morphological weight, indel (gap) cost and tv:ts ratio were varied (Tables 7, 11). *A*, *C*, Strict consensus. *B*, *D*, Majority rule (>50%) consensus. The frequencies with which nodes were retrieved in >50% of the analyses are indicated below the branches for frequencies of >50% but <100%. Nodes retrieved in <50% of the analyses are collapsed. Remaining uncollapsed nodes were retrieved in all analyses.

synapomorphies at each node, is provided in Fig. 8. The length, fit, *CI* and *RI* of the morphological characters on the optimal tree obtained by simultaneous analysis of all the data are provided in Table 12.

Discussion

Scorpionid systematics

All simultaneous analyses confirmed the monophyly of the four scorpionid genera (Fig. 6*A*, *C*), each of which was supported by the following morphological synapomorphies (Fig. 8): 49, 59 and 66 (*Heterometrus*); 3, 4, 8, 22, 47, 54, 73, 77, 92 and 94 (*Opistophthalmus*); 22, 45, 54 and 55 (*Pandinus*); 12, 31, 56, 82, 86, 87, 101–103 and 106 (*Scorpio*). In addition, most simultaneous analyses (including the optimal trees obtained by analyses based on aligned molecular data and direct optimisation), retrieved the following arrangement of scorpionid genera: (*Opistophthalmus* (*Scorpio* (*Heterometrus* + *Pandinus*))). This result contrasts with that of a previous analysis by Prendini (2000*a*), where the following arrangement was obtained for the scorpionid genera (Fig. 1*B*): ((*Opistophthalmus* + *Scorpio*) (*Heterometrus* + *Pandinus*)). However the latter analysis was based on a smaller taxon sample for *Heterometrus*, *Opistophthalmus* and *Pandinus*, as it formed part of a larger analysis of relationships within the superfamily Scorpionoidea, based on exemplar species, and also did not include molecular data. None of the present analyses supported the (*Opistophthalmus* + *Scorpio*) clade.

The (*Heterometrus* + *Pandinus*) clade, proposed by various authors (e.g. Hewitt 1925; Couzijn 1981), and supported by four synapomorphies in the analyses by Prendini (2000*a*), was supported by 19 morphological synapomorphies in the analyses presented here: 20, 23, 26, 32, 37, 39, 43, 44, 48, 57, 63, 65, 67, 69, 84, 85 and 98–100. In contrast, the (*Opistophthalmus* + *Scorpio*) clade was supported by only a single synapomorphy in the analyses by Prendini (2000*a*), whereas the (*Scorpio* (*Heterometrus* + *Pandinus*)) clade was supported by seven morphological synapomorphies in the present analyses: 40, 41, 48, 49, 60, 61 and 76.

The phylogenetic position of *Opistophthalmus*, proposed in the present analyses, supports the views of earlier authors (Hewitt 1925; Lawrence 1928, 1969). Hewitt (1925) contended that *Opistophthalmus* is the most basal member of the Scorpionidae, while recognising that the genus also includes the most specialised members of the family (e.g. the *karrooensis* group). In addition, Hewitt (1925) recognised the close relationship between *Opistophthalmus* and *Scorpio*, citing the prior placement of *O. boehmi* in the latter genus by Kraepelin (1899) as evidence, and maintained that the closely related genera *Pandinus* and *Heterometrus* (as *Palamnaeus*

Table 11. Character incongruence (ILD) among the MPTs obtained by separate analysis of the morphological and molecular data (gaps included) under direct optimisation

W_{Mor} and W_{Mol} denote the weighting schemes for morphological and molecular data, respectively; L_{Mor}, L_{Mol} and L_{Comb} denote the length of the MPT(s) for the morphological, molecular and combined data sets, respectively; Σ denotes the summed lengths of the MPT(s) for the separate data sets. The weighting scheme that minimised character incongruence between the data sets is indicated in bold. ILD values for analyses of the aligned molecular data (gaps included and excluded) under equal weighting are 0.0034 and 0.0030 respectively

W_{Mor}	W_{Mol}	L_{Mor}	L_{Mol}	L_{Comb}	Σ	ILD
1	110	251	740	1020	991	0.0284
1	111	251	1768	2045	2019	0.0127
2	121	502	2534	3087	3036	0.0165
4	141	1004	4031	5133	5035	0.0191
1	210	251	788	1071	1039	0.0299
2	210	502	788	1345	1290	0.0409
1	**211**	**251**	**1824**	**2100**	**2075**	**0.0119**
2	211	502	1824	2376	2326	0.0210
2	221	502	2625	3183	3127	0.0176
4	221	1004	2625	3729	3629	0.0268
4	241	1004	4206	5325	5210	0.0216
8	241	2008	4206	6417	6214	0.0316
1	410	251	861	1148	1112	0.0314
4	410	1004	861	1972	1865	0.0543
1	411	251	1902	2185	2153	0.0146
4	411	1004	1902	3011	2906	0.0349
2	421	502	2775	3347	3277	0.0209
8	421	2008	2775	4995	4783	0.0424
4	441	1004	4503	5649	5507	0.0251
16	441	4016	4503	8943	8519	0.0474

Table 12. Length (steps), fit (F_i), consistency index (*CI*) and retention index (*RI*) of informative morphological characters on the optimal tree obtained by simultaneous analysis of the morphological and aligned molecular data under the weighting regime that maximised fit and minimised length

Numbers in parentheses give corresponding values that differed on the optimal tree obtained by simultaneous analysis of the morphological and optimised molecular data under the weighting regime that minimised character incongruence among the data partitions

Char	Steps	Fit	*CI*	*RI*	Char	Steps	Fit	*CI*	*RI*
1	2 (3)	7.5 (6)	50 (33)	50 (0)	55	3	7.5	66	85
2	3 (4)	6 (5)	33 (25)	50 (25)	56	1	10	100	100
3	1	10	100	100	57	1	10	100	100
4	2	7.5	50	50	59	1	10	100	100
5	2	7.5	50	80	60	3	7.5	66	50
6	2	7.5	50	0	61	2	7.5	50	66
7	1	10	100	100	62	3	6	33	0
8	1	10	100	100	63	2	7.5	50	80
9	1	10	100	100	64	3	7.5	66	80
10	3	7.5	66	0	65	2	10	100	100
11	3	6	33	60	66	3	7.5	66	80
12	2	7.5	50	66	67	4	7.5	75	80
13	2	7.5	50	66	68	2	7.5	50	0
14	2	10	100	100	69	1	10	100	100
15	5	5	40	40	70	2	7.5	50	50
16	2	10	100	100	71	4	6	50	33
17	8 (9)	3.7 (3.3)	37 (33)	37 (25)	72	1	10	100	100
18	10	3	30	22	73	1	10	100	100
19	2	7.5	50	50	74	1	10	100	100
20	2	7.5	50	80	75	4	6	50	33
22	4	6	50	66	76	2	7.5	50	50
23	2	10	100	100	77	3	6	33	33
24	2	7.5	50	0	78	2	7.5	50	0
25	3	6	33	50	79	4	5	25	25
26	2	7.5	50	80	80	3	6	33	33
27	2	7.5	50	66	81	1	10	100	100
28	3	6	33	50	82	3	6	33	33
29	2	7.5	50	50	83	1	10	100	100
30	3	6	33	33	84	3	6	33	50
31	1	10	100	100	85	5	5	40	40
32	6	4.2	33	50	86	2	7.5	50	50
33	2	7.5	50	50	87	2	7.5	50	50
34	1	10	100	100	88	1	10	100	100
35	1	10	100	100	89	4	6	50	0
37	4	6	50	50	90	4	6	50	0
39	4	6	50	75	91	2	7.5	50	0
40	3	6	33	60	92	2	7.5	50	75
41	3	6	33	60	93	9	3	22	12
42	3	6	33	66	94	2	7.5	50	75
43	1	10	100	100	95	3	6	33	0
44	1	10	100	100	96	3	6	33	33
45	2	7.5	50	75	97	6	4.2	33	0
46	2	7.5	50	0	98	2	7.5	50	80
47	2	7.5	50	50	99	2	7.5	50	83
48	2	10	100	100	100	4	6	50	66
49	2	10	100	100	101	3	7.5	66	75
50	3	6	33	33	102	3	7.5	66	66
51	4 (3)	6 (7.5)	50 (66)	33 (66)	103	3	7.5	66	75
52	2	7.5	50	0	105	3	6	33	0
53	2	7.5	50	0	106	1	10	100	100
54	5	6	60	71					

Thorell, 1876), were relatively more specialised. Lawrence (1928, 1969) proposed a similar scenario.

These ideas are concordant with the pectinate arrangement of the scorpionid genera proposed here. However, the notion of these authors that the most basal scorpionids occur in the southern and south-western parts of Africa, followed in regular order by successively more derived species to the north-east (explained by the somewhat teleological thesis that they migrated, or were expelled, as more 'successful' derived forms evolved at the centre of origin in the north-east), is rejected. The latter view is based on outdated orthogenetic concepts, whereas the process is now more parsimoniously understood to be the result of successive vicariance and dispersal events, followed by localised speciation (see Platnick and Nelson 1978; Nelson and Platnick 1981; Nelson and Rosen 1981 and references therein; Poynton 1983, 1986; Humphries and Parenti 1986). Furthermore, as demonstrated in the present analyses, many of the most derived African scorpionids inhabit the south-western arid region, a finding that is congruent with other groups of scorpions, such as the distantly related buthid genus *Parabuthus* Pocock, 1890 (see Prendini 2001*c*). Within *Opistophthalmus*, the two most basal species, *O. boehmi* and *O. lawrencei* Newlands, 1969 inhabit the north-eastern region of southern Africa (extending to East Africa in the case of *O. boehmi*), but this region is also occupied by *O. glabrifrons* Peters, 1861, a derived member of the genus, the distribution of which was used by Hewitt (1925) as evidence for his hypothesis (Prendini 2001*d*).

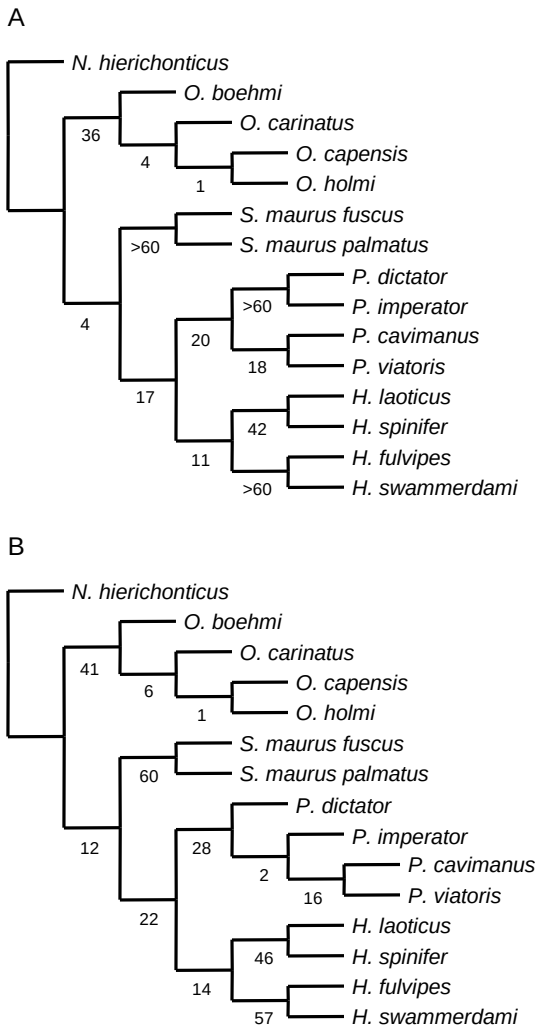

Fig. 7. *A*, The optimal tree obtained by simultaneous analysis of the morphological data (Table 3) and aligned molecular data (Accessory Material) under the weighting regime that minimised length and maximised fit. This MPT was obtained by analysis with implied weights under $k = 6$ and gaps included (Table 10). Branch support values of nodes are provided below branches. *B*, The optimal tree obtained by simultaneous analysis of the morphological data (Table 3) and optimised molecular data under the weighting regime that minimised character incongruence among the data partitions. This MPT was obtained by analysis with costs for indel (gap), tv and ts of 2, 1 and 1, respectively, and morphological data weighted equal to the tv:ts cost (Tables 7, 11). Branch support values of nodes are provided below branches.

Internal relationships within the genus *Opistophthalmus* were the most labile among the various analyses. All separate morphological and simultaneous analyses placed *O. boehmi* basal to the other three exemplar species, confirming previous findings (Prendini 2000*a*), whereas the separate molecular analyses placed *O. holmi* basal. Relationships among *O. capensis*, *O. carinatus* and *O. holmi* remain equivocal, although the optimal trees obtained by the simultaneous analyses both confirm the placements that are recovered in a larger analysis of internal relationships within the genus (Prendini 2001*d*): (*O. carinatus* (*O. capensis* + *O. holmi*)). The weak support obtained for the relationships among the exemplar species in the present analysis must be attributed to the small taxonomic sample (the genus comprises approximately 80 species). However, for the purposes of the present study, it is important to note that species previously placed in the genera *Heterometrus* or *Scorpio*, viz. *O. boehmi* (Kraepelin 1896, 1899; Pocock 1900*b*) and *O. carinatus* (Peters 1861, 1862), were unequivocally placed in *Opistophthalmus*, following Kraepelin (1894, 1913). Similarly, the synonymy of monotypic genera (see Kraepelin 1894; Pocock 1896*a*; Newlands 1972*a*), previously created for various basal or derived species of *Opistophthalmus*, viz. *Petrooicus* Karsch, 1879 and *Oecopetrus* Pocock, 1893 for *O. carinatus* (also see Simon 1888), and *Protophthalmus* Lawrence, 1969 for *O. holmi*, was supported.

Among the four exemplar species chosen to represent the genus *Pandinus*, the East African members of *Pandinus*, represented by *P. cavimanus* and *P. viatoris*, consistently formed a monophyletic group, whereas the relative placements of the West African members, represented by *P. dictator* and *P. imperator*, remained unclear. A pectinate arrangement—reflected in the optimal tree obtained by simultaneous analysis of the morphological and molecular

data with direct optimisation (Fig. 7*B*), and obtained by the majority of separate molecular analyses under direct optimisation (Fig. 5*D*)—suggests that the East African members are relatively derived, compared with the West African members, which appear to be paraphyletic. The basal position of *P. dictator*, retrieved in these analyses, supports Vachon's (1974) contention that this is the most basal member of the genus. The alternative arrangement, whereby *P. dictator* and *P. imperator* form a monophyletic sister-group of the (*P. cavimanus* + *P. viatoris*) group, was obtained by the majority of separate morphological analyses (Fig. 4*B*), as well as the majority of separate molecular and simultaneous analyses (including the optimal tree) based on fixed alignment (Figs 5*B*, 6*B*, 7*A*). This arrangement suggests a monophyletic origin for the West African species, and falsifies Vachon's (1974) hypothesis of a basal position for *P. dictator*, but a detailed phylogenetic analysis of the species of *Pandinus* is required to confirm or reject these findings.

Within the genus *Heterometrus*, two monophyletic groups, representing the two Indian exemplar species (*H. fulvipes* + *H. swammerdami*) and the two South-East Asian exemplar species (*H. laoticus* + *H. spinifer*), were unanimously obtained by the simultaneous analyses (Fig. 6*A*, *C*). This arrangement appears to falsify Couzijn's (1981) hypothesis that *H. swammerdami* is the most basal member of the genus but, as with *Pandinus*, a detailed phylogenetic analysis of the species of *Heterometrus* is required to confirm this finding.

Scorpionid biogeography

The geographical distribution of the scorpionid genera (Fig. 3) has been a topic of discussion for more than a century (Pocock 1894; Kraepelin 1905; Birula 1917*b*; Hewitt 1925; Lawrence 1928, 1969; Vachon 1953; Couzijn 1981; Stockwell 1989; Sissom 1990; Prendini 2000*a*). *Opistophthalmus* and *Pandinus* are endemic to Africa and the Arabian Peninsula. *Scorpio* extends from Senegal and Morocco on the West African coast, along the Mediterranean coast to the Arabian Peninsula, and on through the Middle East as far north as southern Turkey and as far east as central Iran. *Heterometrus* is endemic to India, Sri Lanka and South-East Asia, reaching as far as Wallace's Line.

Besides differences in their geographical distributions, the four genera differ fundamentally in the habitats that they occupy. Most species of *Heterometrus* (including the most basal), as well as the most basal species of *Pandinus*, inhabit tropical rainforest habitats and mesic savanna. Only the relatively derived species of *Pandinus* inhabit semi-arid savanna and semi-desert (in East Africa), which appears to be a secondary specialisation. *Scorpio* inhabits Mediterranean habitats (experiencing summer drought) and semi-desert, while *Opistophthalmus* inhabits semi-arid savanna and karoo, as well as arid to hyper-arid desert habitats. Thus, there is a clear difference between the genera that inhabit mostly mesic habitats (*Heterometrus* and *Pandinus*) and those that inhabit semi-arid to hyper-arid habitats (*Scorpio* and *Opistophthalmus*). Mesic habitats, especially tropical

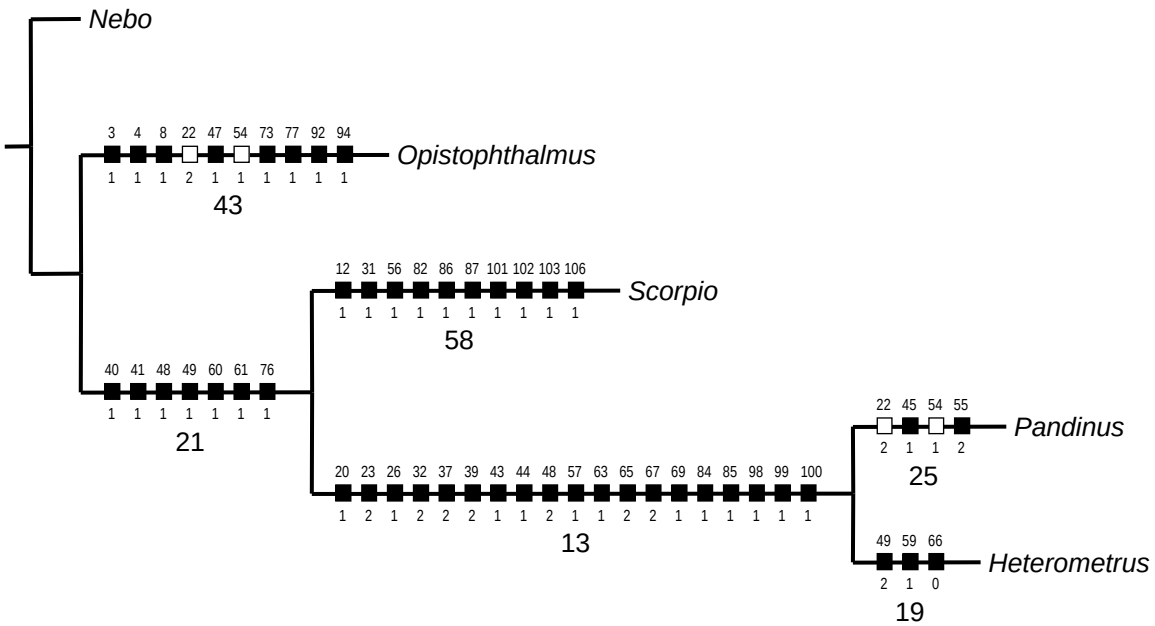

Fig. 8. Summary cladogram indicating the most parsimonious reconstruction of relationships among the four genera of Scorpionidae. ■, Uniquely derived apomorphic states; □, parallel derivations of apomorphic states (unambiguously optimised changes only). The number above each bar gives the character number, and the number below gives the character state. Numbers below branches provide the count of molecular synapomorphies (gaps included) for each genus. Refer to Appendix 2 for character descriptions.

and temperate forests, are regarded as ancestral in the Scorpionidae on the basis of the occurrence of all more basal scorpionoids in such habitats. The most basal genera of Bothriuridae, the Heteroscorpionidae, the most basal species of Urodacidae, most Ischnuridae and many Diplocentridae (including the most basal) inhabit forests, or similarly mesic habitats (including caves), whereas arid habitats are inhabited, without exception, by derived members of these families. Accordingly, it is clear that evolution in the Scorpionidae is inextricably linked to the evolution of aridity in Africa and its Gondwanaland precursor.

As discussed above, the phylogenetic positions of the scorpionid genera, as revealed by the present analyses, concord with those hypothesised by earlier authors (Hewitt 1925; Lawrence 1928, 1969), but previous scenarios postulated to account for their distribution are rejected. Hewitt (1925) proposed that the evolution of *Pandinus* in tropical Africa resulted in separation of the original scorpionid 'stock', initially spread throughout Africa, into two sections—*Opistophthalmus* in the south and *Scorpio* in the north—through replacement by the more specialised *Pandinus*, a hypothesis that was elaborated by Lawrence (1928). Hewitt (1925) remained uncertain as to whether the (*Heterometrus* + *Pandinus*) group originated in Africa or Asia, but noted that *Pandinus* was more derived in several respects.

Because the scenarios of Hewitt (1925) and Lawrence (1928) were proposed in the context of a dispersalist, centre-of-origin paradigm, and fail to account for geological events now widely accepted, a revised scenario is hereby proposed to explain the evolution and historical biogeography of the scorpionid genera. First, given that the distributions of *Pandinus* and *Heterometrus* in Africa and Asia, respectively, are now understood to be the result of vicariance induced by continental drift, a concept not generally accepted at the time of Hewitt (1925) and Lawrence's (1928) papers, the origin of this group must pre-date the mid to late Cretaceous separation of the Indian plate from Africa (Smith and Hallum 1970; Embleton and McElhinny 1975; Smith 1976) as argued by Couzijn (1981), Stockwell (1989) and Sissom (1990). Second, the phylogenetic positions of *Opistophthalmus* and *Scorpio*, basal to the (*Heterometrus* + *Pandinus*) group, imply that the evolution of their common ancestor (i.e. the common ancestor of the Scorpionidae) must also pre-date this separation, in line with the hypothesis of Stockwell (1989). In view of the present distributions of the most basal species of *Opistophthalmus* and the majority of *Pandinus* species in north-east Africa, on one hand, and the most basal species of *Heterometrus* in Sri Lanka and south-west India, on the other, the eastern Gondwanaland origin for the Scorpionidae, proposed by Sissom (1990), is plausible. On this premise, and given the proposed phylogenetic relationships among the genera, initial divergence of the common ancestors of *Opistophthalmus* and *Scorpio*, from the common ancestor of the (*Heterometrus* + *Pandinus*) group, must have occurred in eastern Gondwanaland, presumably under semi-arid conditions that already existed before its break-up, that is, the 'Gondwana Desert' and surrounding semi-arid areas (Irish 1990; Pickford and Senut 2000). Subsequent evolution and radiation of *Opistophthalmus* from its Gondwanaland ancestor must be explained as an effect of adaptation to increasingly arid conditions in southern and eastern Africa that began in the Eocene and had developed to their fullest extent by the late Pliocene (van Zinderen Bakker 1975; Ward *et al.* 1983; Deacon and Lancaster 1988; Ward and Corbett 1990). The evolution of *Scorpio* from its Gondwanaland ancestor could be attributed to the more recent onset of aridification of northern Africa, which was covered by lowland rainforest—the ancestral habitat of the Scorpionidae—throughout most of the Tertiary (Axelrod and Raven 1978). Presumably, this genus diversified during the Oligo-Miocene, under somewhat more mesic conditions (i.e. savanna) than at present (Axelrod and Raven 1978), and was more widespread across northern Africa until the advent of hyper-arid conditions during the late Miocene to early Pliocene (van Zinderen Bakker 1978, 1979, 1980; Pickford and Senut 2000), at which stage it contracted to its present relictual distribution, along with various other Saharan taxa (Niethammer 1971; Dumont 1982).

Taxonomy

Family **SCORPIONIDAE** Latreille

Scorpionides Latreille, 1802: 46, 47 (part)[1]; 1804: 110 (part); 1806: 130 (part); 1810: 116, 118 (part); Leach, 1814: 412; 1815: 390; Latreille, 1817: 310 ('tribe'; part); 1825: 310 ('tribe'; part); Sundevall, 1833: 29 (part). Type genus: *Scorpio* Linnaeus, 1758.

Scorpiones: Ehrenberg in Hemprich & Ehrenberg, 1828: pl. I, figs 1, 2 (family; part).

Buthides C. L. Koch 1837: 36, 37 (part).

Centrurides C. L. Koch, 1837: 38 (part). Type genus: *Centrurus* Ehrenberg, 1829 [= *Heterometrus* Ehrenberg, 1828].

Scorpionini: Peters, 1861: 510 (part); Lankester, 1885: 379 (subfamily; part); Pocock, 1893: 305 (subfamily); Kraepelin, 1894: 24 (subfamily); Laurie, 1896*b*: 128 (subfamily).

Pandinoidae Thorell, 1876*a*: 11 (part); 1876*b*: 83 (part); Karsch, 1879*a*: 19 (part); Thorell & Lindström, 1885: 25 (part). Type genus: *Pandinus* Thorell, 1876*a*.

Pandinini (subfamily): Thorell, 1876*a*: 11 (part); 1876*b*: 84 (part); Karsch, 1879*a*: 19 (part); Thorell & Lindström, 1885: 25 (part).

Heterometridae Simon, 1879: 92, 115. Type genus: *Heterometrus* Ehrenberg, 1828 (part) [= *Scorpio* Linnaeus, 1758][2].

Scorpionidae: Lankester, 1885: 379 (part); Pocock, 1893: 305, 306 (part); Kraepelin, 1894: 8 (part); Laurie, 1896*b*: 128 (part); Kraepelin, 1899: 96 (part); Pocock, 1900*a*: 84; Kraepelin, 1905: 343 (part); 1913: 165; Birula ,1917*a*: 161 (part); 1917*b*: 58, 59 (part); Pavlovsky, 1924*b*: 78 (part); 1925: 190, 191, 195 (part); Werner. 1934: 275 (part); Kästner, 1941: 232 (part); Millot & Vachon, 1949: 428 (part); Petrunkevitch, 1955: P75; Bücherl, 1964: 59 (part); 1967: 114 (part); Stahnke, 1974: 339 (part); L. E. Koch, 1977: 159 (part); Lamoral, 1980: 440 (part); Levy & Amitai, 1980: 102 (part); Tikader & Bastawade, 1983: 517, 518; Francke, 1982*b*: 75 (part); 1985: 18; Lourenço, 1989: 161,

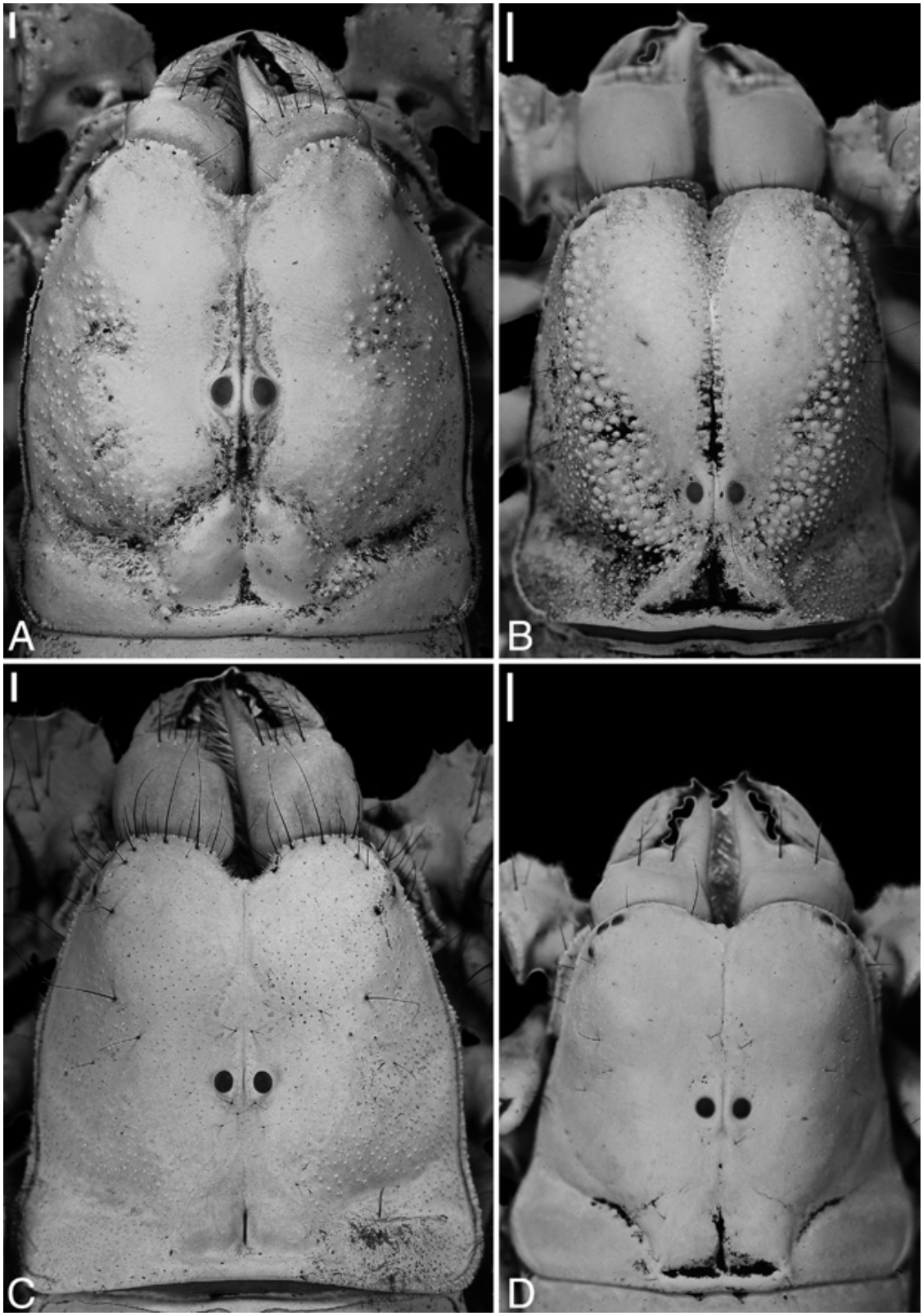

Fig. 9. Carapaces of representative scorpionids, illustrating ocelli, sulci and surface macrosculpture in dorsal aspect. *A*, *Heterometrus spinifer* (Ehrenberg, 1828), ♀ (AMNH). *B*, *Opistophthalmus capensis* (Herbst, 1800), ♂ (AMNH). *C*, *Pandinus imperator* (C. L. Koch, 1841), ♂ (AMNH). *D*, *Scorpio maurus palmatus* (Ehrenberg, 1828), ♀ (AMNH). Scale bars = 1 mm.

174; Sissom, 1990: 131; Nenilin & Fet, 1992: 5 (part); Kovařík, 1997: 183; 1998: 136; Lourenço, 1999: 929 (part); Fet, 2000: 427, 428 (part); Prendini, 2000*a*: 34, 35, 39, 44; Lourenço, 2000: 25.

Pandinidae: Marx, 1890: 211.

Scorpioninae: Kraepelin, 1899: 106; 1905: 344; Birula, 1917*a*: 161; 1917*b*: 59; Pavlovsky, 1924*b*: 78, 79; 1925: 192; Werner, 1934: 277; Kästner, 1941: 233; Millot & Vachon, 1949: 428; Bücherl, 1964: 59; Lamoral, 1979: 668; Levy & Amitai, 1980: 102; Tikader & Bastawade, 1983: 518; Lourenço, 1989: 174; Sissom, 1990: 131; Fet, 2000: 430, 431.

Scorpionaria: ('tribus') Birula, 1917*a*: 161.

Diagnosis

The Scorpionidae can be placed unequivocally in the superfamily Scorpionoidea Latreille, 1802 on the basis of the following characters (Prendini 2000*a*): retrolateral pedal spurs of telotarsi absent; ventrosubmedian macrosetae of telotarsi spiniform; genital opercula (♀) fused along the midline; paraxial organ (♂) with an internobasal reflection of the sperm duct. Additional characters that, in combination, place the Scorpionidae unequivocally in the Scorpionoidea, are as follows (Stockwell 1989; Prendini 2000*a*): cheliceral movable finger with one subdistal tooth and without serrula; Type C trichobothrial pattern (femur with 3 trichobothria; patella with 19 or more; chela with 26 or more); hemispermatophore lamelliform with a distinct truncal flexure.

The Scorpionidae can be separated from all other scorpionoid taxa by the following character: pedipalp chela with dorsal secondary carina partially developed, extending part-way across dorsal surface of manus, and subdigital carina partially developed, extending part-way across in opposite direction. They can also be separated from all other scorpionoid taxa, except the Diplocentrinae, by the following characters: pedipalp chela with ventromedian carina more strongly developed than ventrointernal and internomedian carinae; ventrointernal and internomedian carinae equally developed (often obsolete); pedipalp patella with trichobothrium d_2 located on internal surface.

Characters separating this family from particular scorpionoid families are as follows (Stockwell 1989; Prendini 2000*a*): presence of ovariuterine diverticula separates Scorpionidae from Bothriuridae; paired ventrosubmedian carinae of metasomal segments I–IV separates Scorpionidae from Hemiscorpiidae and Urodacidae; rounded laterodistal lobes of the telotarsi separates Scorpionidae from Ischnuridae; absence of a subaculear tubercle separates Scorpionidae from Diplocentridae.

Description

The following account is distilled from the most recent description provided by Prendini (2000*a*), with new observations added where available.

Colour. Varies from entirely dark brown or black (with or without pale legs and telson) in *Heterometrus* and *Pandinus*, some *Opistophthalmus* and *Scorpio* to entirely pale in some *Opistophthalmus* and *Scorpio*. Combinations of dark tergites (with or without dark sternites and metasoma), pale legs and pale carapace and/or pedipalps in many *Opistophthalmus*.

Carapace. Median notch usually present in anterior margin, deep in *Heterometrus* and *Pandinus* (Fig. 9*A*, *C*), shallow in *Scorpio* and *Opistophthalmus* (Fig. 9*B*, *D*), rarely absent (some *Opistophthalmus*); rostrolateral margin with or without a distinct notch next to posterior lateral ocelli. Median longitudinal sulcus suturiform, often with anterior furcation (sutures absent in some *Opistophthalmus*); anteromedian and anterocular depressions may also be present (*Opistophthalmus*). Posterior carapacial sutures present (absent in some *Opistophthalmus*). Three pairs of lateral ocelli (rarely two in some *Opistophthalmus*). Median ocular tubercle raised (secondarily shallow in *Scorpio* and some *Opistophthalmus*), usually situated medially to posteromedially (but varying from anteromedial to extremely posterior in *Opistophthalmus*); superciliary carinae usually higher than ocelli (but lower in *Scorpio* and some *Opistophthalmus*), and often extended anteriorly (*Heterometrus*, some *Opistophthalmus*) and posteriorly (*Heterometrus*). Surfaces of carapace finely to coarsely granular laterally, smooth to coarsely granular in interocular region, and smooth to coarsely granular posteromedially.

Chelicerae. Cheliceral fixed finger with medial and basal teeth fused into a bicusp (Fig. 10). Movable finger with one subdistal tooth and one basal tooth on external margin; distal external and distal internal teeth unequal, distal external tooth slightly to considerably smaller than distal internal tooth, usually aligned longitudinally and not opposable (moderately opposable in some *Heterometrus*, *Opistophthalmus* and *Pandinus*); distal internal margin smooth (without serrula). Cheliceral coxae with stridulatory setae (scaphotrix) on dorsointernal surfaces and chemoreceptive lamelliform setae (trichocopae) on internomedian surfaces (*Opistophthalmus*, Fig. 10*C*, *D*) or without these setae (*Heterometrus*, *Pandinus*, *Scorpio*, Fig. 10*A*, *B*, *E–H*).

Pedipalps. Chela sparsely to densely setose, especially in adult ♂, surface macrosculpture varying from smooth or reticulate to coarsely granular (Figs 11–14). Chela with 10 carinae, only one of which (the ventroexternal carina) is always distinct. Dorsal secondary carina partially developed, extending part-way across dorsal surface of manus; subdigital carina partially developed, extending part-way across in opposite direction; dorsal secondary and subdigital carinae distinct (*Scorpio* and most *Opistophthalmus*) or obsolete (*Heterometrus*, *Pandinus* and some *Opistophthalmus*); digital carina distinct (most *Opistophthalmus* and *Scorpio*) or obsolete (*Heterometrus*, *Pandinus* and some *Opistophthalmus*); ventroexternal carina distinct, parallel to longitudinal axis of chela, with distal

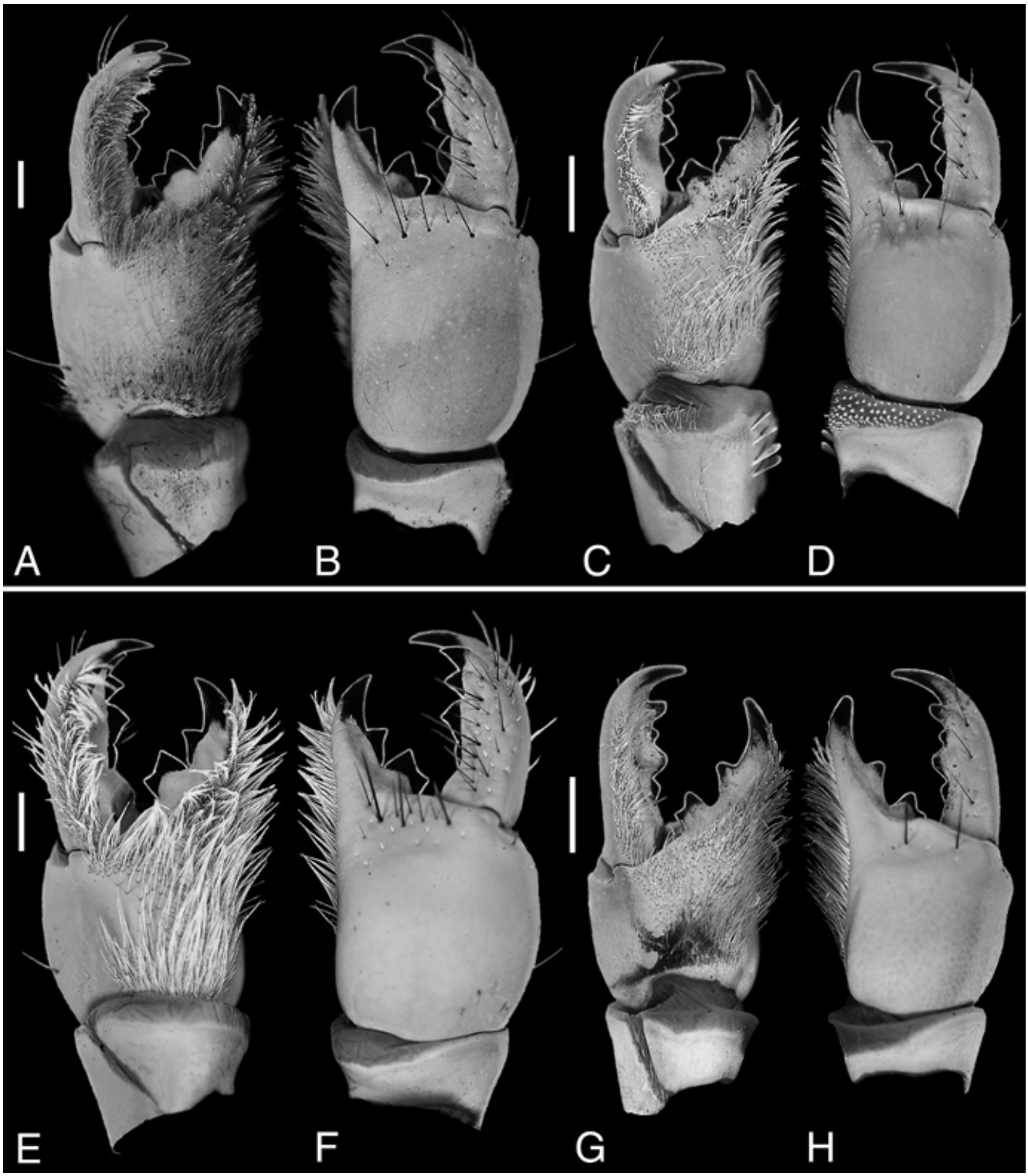

Fig. 10. Dextral chelicerae of representative scorpionids, illustrating dentition and macrosetae in ventral (*A*, *C*, *E*, *G*) and dorsal (*B*, *D*, *F*, *H*) aspects. *A*, *B*, *Heterometrus spinifer* (Ehrenberg, 1828), ♀ (AMNH). *C*, *D*, *Opistophthalmus capensis* (Herbst, 1800), ♂ (AMNH). *E*, *F*, *Pandinus imperator* (C. L. Koch, 1841), ♂ (AMNH). *G*, *H*, *Scorpio maurus palmatus* (Ehrenberg, 1828), ♀ (AMNH). Scale bars = 1 mm.

edge directed toward a point between external and internal movable finger condyles, but closer to external condyle; ventromedian carina more strongly developed than ventrointernal and internomedian carinae (obsolete in *Heterometrus* and *Pandinus*); ventrointernal and internomedian carinae equally developed (usually obsolete). Chela fingers smooth (*Scorpio* and most *Opistophthalmus*) or granular (*Heterometrus*, *Pandinus* and some *Opistophthalmus*); each with a single primary row of denticles along the cutting edge; terminal denticles interlocking unevenly when closed (movable finger displaced to exterior), externodistal edge of fixed finger with notch for terminal denticle of movable finger; fingers often with six enlarged granular lobes and with second lobe of movable finger (♂) more strongly developed than other lobes, with correspondingly well-developed notch in fixed finger (*Heterometrus*, *Pandinus* and some *Opistophthalmus*), or not larger than other lobes (*Scorpio*, most *Opistophthalmus*).

Patella with eight carinae, not all of which are distinct in all taxa (Figs 15, 16). Patella usually with anterior process obsolete and dorsal surface convex, dorsomedian carina raised above horizontal axis of dorsoexternal carina (but with anterior process moderately developed and dorsal surface flat, dorsomedian and dorsoexternal carina in same axis, in some *Opistophthalmus*); dorsomedian carina distinct (*Scorpio*, most *Opistophthalmus*) or obsolete (*Heterometrus*, *Pandinus* and some *Opistophthalmus*); dorsoexternal and internomedian carinae usually obsolete (but moderately to well developed in some *Heterometrus*, *Pandinus* and *Opistophthalmus*); ventroexternal and paired externomedian carinae distinct (*Scorpio*, most *Opistophthalmus*) or obsolete (*Heterometrus*, *Pandinus* and some *Opistophthalmus*).

Femur with six carinae, three of which (the dorsoexternal, internomedian and ventrointernal carinae) are always distinct. Femur dorsoexternal carina more (*Heterometrus* and *Pandinus*) or less (*Opistophthalmus* and *Scorpio*) strongly developed than dorsointernal carina, which may be obsolete or absent (*Pandinus*); internomedian carina usually oriented diagonally between ventrointernal and dorsointernal carinae (but oriented parallel to dorsointernal and ventrointernal carinae in some *Opistophthalmus*); ventroexternal and ventroexternal secondary carinae absent (*Heterometrus*, *Pandinus*, *Scorpio* and some *Opistophthalmus*) or present (most *Opistophthalmus*).

Trichobothria. Pedipalps type C orthobothriotaxic (*Heterometrus* and *Scorpio*, Figs 11, 14, 15*A–C*, 16*D–F*) or neobothriotaxic major (*Opistophthalmus* and *Pandinus*, Figs 12, 13, 15*D–F*, 16*A–C*), with accessory trichobothria in the *v* and *e* series of the patella, the *V* series of the chela, and the *i* series of the chela (some *Pandinus* only). Femur with trichobothrium *i* located on dorsal surface or internal surface (*Scorpio* only). Patella with trichobothrium d_2 located on internal surface. Chela with trichobothria *ib* and *it* located basally on fixed finger; *db* located on internal surface of fixed finger; *eb* located proximally on fixed finger; *esb* located midway along fixed finger, level with *eb–est–et*; *Db* located on dorsal surface of manus; *Dt* located distally on manus, near base of fixed finger; *Est* located distally on manus; Et_2 located on external surface of manus; V_2 and V_3 not widely separated.

Pectines. Internal fulcral plates setose. First proximal median lamella of each pecten usually with mesial margin angular and pectinal teeth present along entire posterior margin (with mesial margin shallowly curved and proximal region of posterior margin devoid of teeth in some *Opistophthalmus* and *Pandinus*). Pectinal teeth (♂) straight and elongate (*Heterometrus*, *Pandinus* and some *Opistophthalmus*) or short and curved (*Scorpio*, most *Opistophthalmus*).

Sternum. Sternum longer than wide, pentagonal to subpentagonal. Median longitudinal sulcus shallow anteriorly, deep and narrow posteriorly.

Genital operculum. Genital opercula of ♂ separate (usually overlapping partially in *Heterometrus* and *Pandinus*), of ♀ fused.

Legs. First pair of maxillary lobes (coxapophyses) usually rounded–truncate anteriorly and roughly equal in length to second pair (but tapering anteriorly, longer than, and encircling second pair in some *Heterometrus*, *Opistophthalmus* and *Pandinus*). Stridulatory organs, comprising a 'rasp' (granular tubercles) and 'scraper' (stridulatory setae or scaphotrix), present on opposing surfaces of coxae of pedipalps and first pair of legs (*Heterometrus* and *Pandinus*, Figs 17*A*, *B*, 18*A*, *B*) or absent (*Opistophthalmus* and *Scorpio*[3], Figs 17*C*, *D*, 18*C*, *D*). Tibiae I and II usually each with a retrolateral row of spiniform macrosetae (absent in *Heterometrus* and setiform in some *Opistophthalmus*); tibial spurs absent (Figs 19, 20). Basitarsi I and II each with a retrolateral row of spiniform macrosetae (setiform in some *Opistophthalmus*); prolateral pedal spurs present; retrolateral pedal spurs absent. Telotarsi I–IV usually short, stout and distally broadened in dorsal and lateral views, with dorsomedian lobe approximately equal to laterodistal lobes (but long, narrow, parallel sided in dorsal and lateral views, with dorsomedian lobe considerably shorter than laterodistal lobes in some *Opistophthalmus*); laterodistal lobes rounded, not flush with base of median dorsal lobe; telotarsi each with paired ventrosubmedian rows of spiniform macrosetae (prolateral row absent in many *Opistophthalmus*; Fig. 19*H*), but without a ventromedian row (except, occasionally, at the base); counts of ventrosubmedian spiniform macrosetae equal on telotarsi I–II and III–IV (*Heterometrus* and *Pandinus*) or increasing from I–II to III–IV (*Opistophthalmus* and *Scorpio*).

Mesosoma. Nongranular surfaces smooth to weakly punctate. Pre-tergites smooth. Post-tergites smooth, finely or coarsely granular. Sternites usually smooth (♂, ♀), but

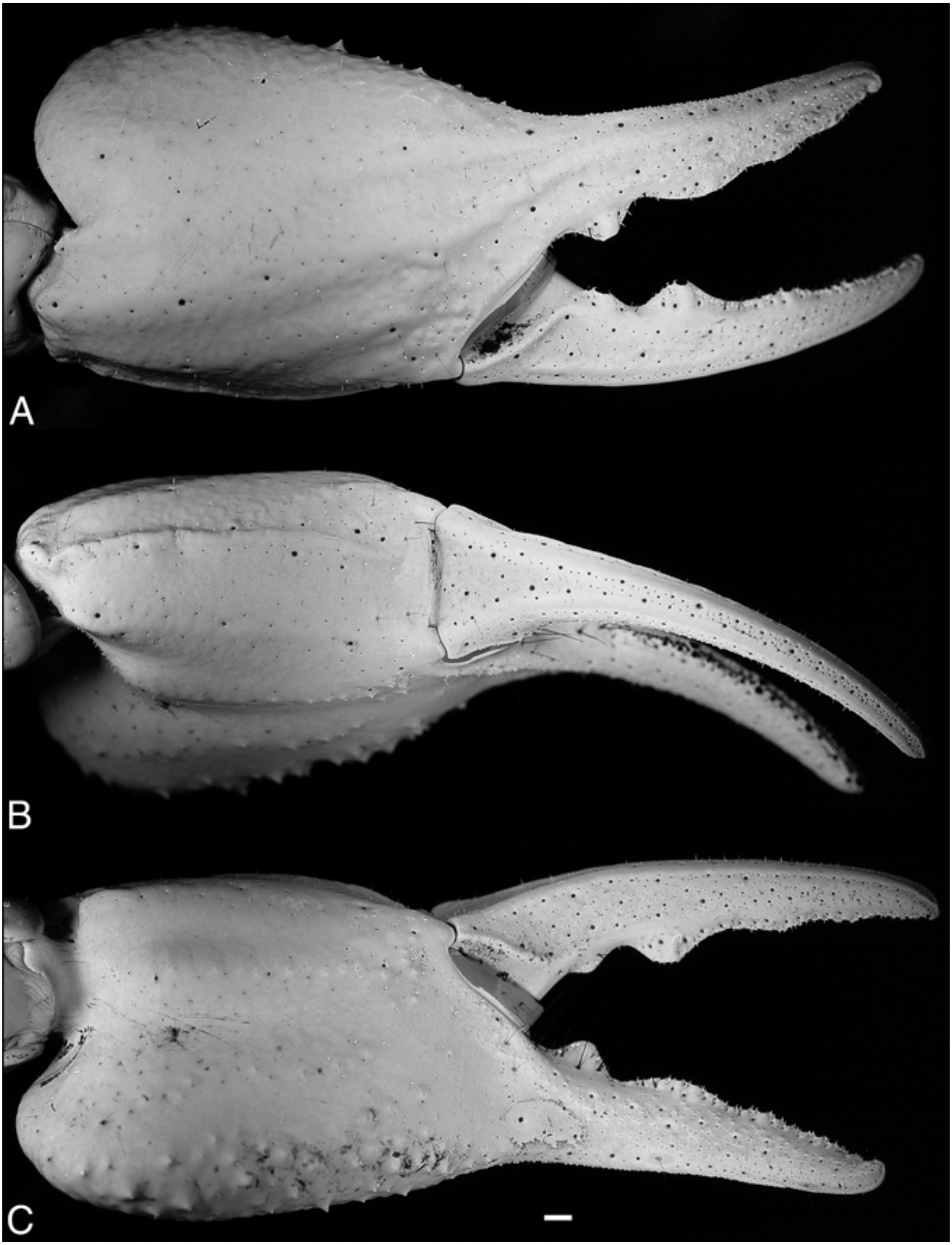

Fig. 11. Dextral pedipalp chela of *Heterometrus spinifer* (Ehrenberg, 1828), ♀ (AMNH), illustrating trichobothria, macrosetae and surface macrosculpture in dorsoexternal (*A*), ventral (*B*) and internal (*C*) aspects. Scale bar = 1 mm.

III–VI rugose (♂ only) in *Scorpio*, III–VII rugose (♂ only) in some *Opistophthalmus*, such as *O. cavimanus* Lawrence, 1928, and III–VII or VII only, granular or tuberculate (♂ and, more rarely, ♀) in *Scorpio*, many *Opistophthalmus* and some *Pandinus*, such as *P. colei* (Pocock, 1896). Sternite VII usually acarinate or with a pair of obsolete ventrolateral carinae (Fig. 21*A–C*), but with four strongly developed carinae (paired ventrosubmedian and ventrolateral) in *Scorpio*, *O. boehmi* and some *Pandinus*, such as *P. cavimanus* (Fig. 21*D*).

Metasoma and telson. Metasomal segments I–IV each with paired ventrosubmedian and ventrolateral carinae (obsolete or absent in some *Opistophthalmus*; Fig. 21*B*), usually equally developed on all segments (Fig. 21*A*, *C*), but

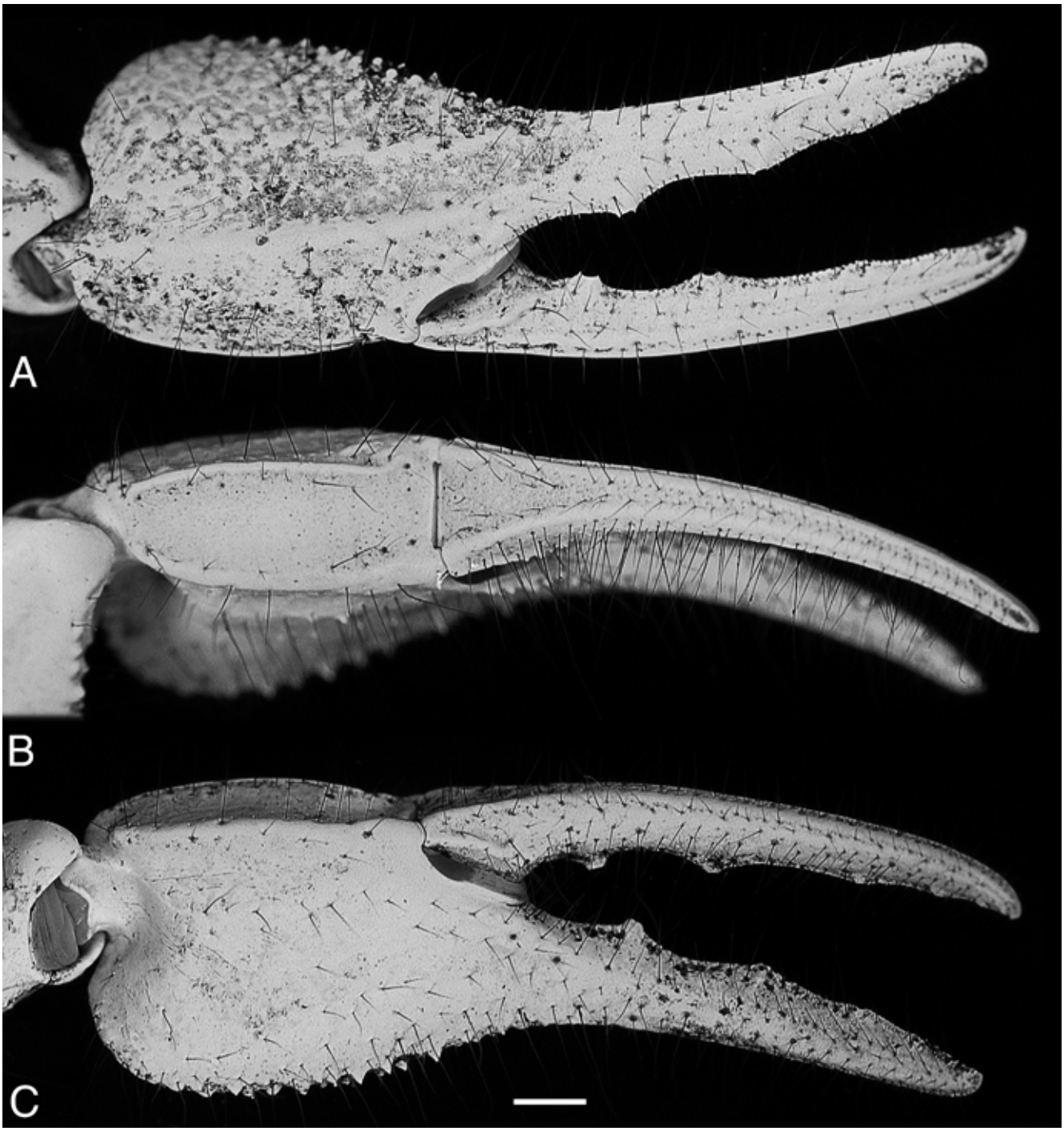

Fig. 12. Dextral pedipalp chela of *Opistophthalmus capensis* (Herbst, 1800), ♂ (AMNH), illustrating trichobothria, macrosetae and surface macrosculpture in dorsoexternal (*A*), ventral (*B*) and internal (*C*) aspects. Scale bar = 1 mm.

more strongly developed on segments III and IV in most *Opistophthalmus*, and more strongly developed on segments I and II in *Scorpio*, *O. boehmi* and some *Pandinus*, such as *P. cavimanus* (Fig. 21*D*); dorsal and lateral surfaces smooth or granular; ventral surfaces usually smooth or granular (♂, ♀), but rugose (♂ only) in some *Opistophthalmus*, such as *O. cavimanus*, or tuberculate (♂ and, more rarely, ♀) in many *Opistophthalmus* and some *Pandinus*, for example *P. colei*. Segment V smooth or granular dorsally, granular ventrally; without a transverse carina, with ventrolateral carinae comprising rounded granules or spiniform denticles, and with distal portion of ventromedian carina continuous, bifurcating or breaking up into numerous granules (*Scorpio* and *O. boehmi*). Telson vesicle not laterally compressed, without anterodorsal lateral lobes, granular ventrally and, occasionally, laterally, to entirely smooth (some *Opistophthalmus*); aculeus long, shallowly curved, without subaculear tubercle. Venom glands complex; venom pigment opalescent.

Male reproductive anatomy. Paraxial organ without semilunar shelf on internal wall of sperm duct invagination; internobasal reflection well developed; accessory glands absent. Hemispermatophore lamelliform, bearing an elaborate capsule; lamellar hook and median lobe separate; distal lamina truncate distally (or rarely tapering in *Opistophthalmus*) and without a prominent sclerotised crest.

Female reproductive anatomy. Ovariuterus forming a reticulate mesh of six cells. Ovariuterine follicles with diverticula.

Embryonic development. Katoikogenic (embryos develop in diverticula of the ovariuterus and obtain nutrition through specialised connections with digestive caeca).

Included taxa

Four extant genera: *Heterometrus* Ehrenberg, 1828; *Opistophthalmus* C. L. Koch, 1837; *Pandinus* Thorell, 1876; *Scorpio* Linnaeus, 1758. Two fossil genera from the Miocene (*Mioscorpio* Kjellesvig-Waering, 1986 from Germany and *Sinoscorpius* Hong, 1983 from China) have been placed in the Scorpionidae by some authors (Kjellesvig-Waering 1986; Sissom 1990; Fet 2000), but this remains to be tested cladistically (Stockwell 1989; Jeram 1994).

Distribution

Africa: Algeria, Angola, Benin, Botswana, Burkina Faso, Cameroon, Central African Republic, Chad, Congo, Côte d'Ivoire, Democratic Republic of Congo, Egypt, Equatorial Guinea (including Bioko Island), Eritrea, Ethiopia, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Kenya, Lesotho, Liberia, Libya, Malawi, Mali, Mauritania, Morocco, Mozambique, Namibia, Nigeria, Senegal, Sierra Leone, Somalia, South Africa, Sudan, Swaziland, Tanzania, Togo, Tunisia, Zambia, Zimbabwe. Asia: Bangladesh, Bhutan, Brunei, Cambodia, India (including Lesser Nikobar Islands), Indonesia, Iran, Iraq, Israel, Jordan, Kuwait, Laos, Lebanon, Malaysia, Myanmar, Nepal, Philippines, Qatar, Saudi Arabia, Singapore, Sri Lanka, Syria, Thailand, Turkey, Vietnam, Yemen.

Heterometrus is endemic to Asia (Fig. 3), reaching greatest species richness and endemism in India, followed by Indonesia (Table 2; counts include subspecies). *Opistophthalmus* is endemic to Africa, reaching greatest species richness and endemism in South Africa, followed by Namibia. *Pandinus* is near-endemic to Africa (including the Arabian Peninsula), and reaches greatest species richness and endemism in Somalia. *Scorpio* is the most widespread scorpionid genus, extending across north Africa to central Asia, but its greatest (sub)species richness and endemism occurs in Morocco. No more than two scorpionid genera occur in any country and the greatest scorpionid species richness and endemism occurs in South Africa.

Key to the genera of the family Scorpionidae

Modified from Sissom (1990).

1. Stridulatory organs, comprising a 'rasp' (granular tubercles) and 'scraper' (stridulatory setae or scaphotrix), present on opposing surfaces of coxae of pedipalps and first pair of legs (Figs 17*A*, *B*, 18*A*, *B*); counts of ventrosubmedian spiniform macrosetae equal on telotarsi I–II and III–IV (Figs 19*A–D*, 20*A–D*) 2
   Stridulatory organs absent from opposing surfaces of coxae of pedipalps and first pair of legs (Figs 17*C*, *D*, 18*C*, *D*); counts of ventrosubmedian spiniform macrosetae increasing from telotarsi I–II to III–IV (Figs 19*E–H*, 20*E–H*) 3
2. Pedipalps orthobothriotaxic, with 26 trichobothria (patella with 13 trichobothria in *e* series and 3 trichobothria in *v* series; chela with 4 trichobothria in *V* series and 2 trichobothria in *i* series; Figs 11, 15*A–C*); granular tubercles of 'rasp' and stridulatory setae (scaphotrix) of 'scraper' situated on coxae of first leg and pedipalp, respectively (Fig. 17*A*, *B*) . . . . . *Heterometrus*
   Pedipalps neobothriotaxic major, with more than 26 trichobothria (patella with more than 13 trichobothria in *e* series and more than 3 trichobothria in *v* series; chela usually with more than 4 trichobothria in *V* series and occasionally with more than 2 trichobothria in *i* series; Figs 13, 16*A–C*); granular tubercles of 'rasp' and stridulatory setae (scaphotrix) of 'scraper' situated on coxae of pedipalp and first leg, respectively (Fig. 18*A*, *B*) . . . . . *Pandinus*
3. Pedipalps neobothriotaxic, with more than 26 trichobothria (patella with more than 13 trichobothria in *e* series and often more than 3 trichobothria in *v* series; chela rarely with more than 4 trichobothria in *V* series; Figs 12, 15*D–F*); cheliceral coxae usually with stridulatory setae (scaphotrix) on dorsointernal surfaces and chemoreceptive lamelliform setae (trichocopae) on internomedian surfaces (Fig. 10*C*, *D*) . . . . . *Opistophthalmus*
   Pedipalps orthobothriotaxic, with 26 trichobothria (patella with 13 trichobothria in *e* series and 3 trichobothria in *v* series; chela with 4 trichobothria in *V* series, Figs 14, 16*D–F*); cheliceral coxae without stridulatory setae (scaphotrix) on dorsointernal surfaces and without chemoreceptive lamelliform setae (trichocopae) on internomedian surfaces (Fig. 10*G*, *H*) . . . . . *Scorpio*

Genus ***Heterometrus*** Ehrenberg

Buthus (*Heterometrus*) Ehrenberg in Hemprich & Ehrenberg, 1828: pl. I, figs 1, 2 (part, only fig. 2); Hemprich and Ehrenberg, 1829: 351, 352; 1831 [unpaginated]. Type species, by subsequent designation (Karsch 1879*a*: 20): *Buthus* (*Heterometrus*) *spinifer* Ehrenberg, 1828 [= *Heterometrus spinifer* (Ehrenberg, 1828)].

Centrurus Ehrenberg in Hemprich & Ehrenberg, 1829: 350. Type species, by monotypy: *Centrurus galbineus* C. L. Koch, 1838 [= *Heterometrus longimanus* (Herbst, 1800)][4].

Buthus (*Heterometros*): Hemprich & Ehrenberg, 1829: 351.

Palamnaeus Thorell, 1876*a*: 13; 1876*b*: 84; Pocock, 1892: 38 (part); 1893: 307 (part); Laurie, 1896*a*: 193; 1896*b*: 128; Pocock, 1896*c*: 77; 1900*a*: 84. Type species, by original designation: *Palamnaeus petersii* Thorell, 1876 [= *Heterometrus petersii* (Thorell, 1876)]. Synonymised: Karsch, 1879*a*: 20.

Caucon Karsch, 1879*a*: 14. Type species, by original designation: *Centrurus galbineus* C. L. Koch, 1838 [= *Heterometrus longimanus* (Herbst, 1800)]. Synonymised: Kraepelin, 1894: 34.

Heterometrus: Karsch, 1879*a*: 20; Laurie, 1896*a*: 193; 1896*b*: 128; Kraepelin, 1899: 107; 1913: 165; Birula 1917*a*: 161; 1917*b*: 59; Werner, 1934: 277; Kästner, 1941: 233; Vachon, 1953: 9, fig. 1; 1963: 162, fig. 4; Bücherl, 1964: 59; Couzijn, 1978: 330; 1981: 73; Tikader & Bastawade, 1983: 518, 519; Francke, 1985: 8, 18; Lourenço, 1989: 174; Sissom, 1990: 131; Nenilin & Fet, 1992: 19, 20; Braunwalder & Fet, 1998: 31; Kovařík, 1998: 136; Fet, 2000: 431; Lourenço, 2000: 25; Prendini, 2000*a*: 44.

Scorpio (*Buthus*) (misidentification; *nec* Leach, 1815): Lankester, 1885: 379.

Scorpio (misidentification; *nec* Linnaeus, 1758): Laurie, 1896*a*: 193; Lönnberg, 1897: 197 (part).

Along with its sister-genus, *Pandinus*, the genus *Heterometrus* includes some of the largest extant scorpions, such as *H. swammerdami*, which can reach 168 mm in length (Couzijn 1981; Sissom 1990). Couzijn (1981) published a monographic revision with keys, wherein 21 species and 31 subspecies (including nine nominotypical forms) were recognised, and classified into five subgenera, on the basis of a manually constructed cladogram. Tikader and Bastawade (1983) subsequently published redescriptions and keys for all the Indian species, and described two new ones. Although they examined many of the same specimens, Tikader and Bastawade (1983) differed from Couzijn (1981) in their opinions on the rank or validity of various taxa, such that 30 species and 27 subspecies (including eight nominotypical forms) are currently recognised (Fet 2000). However, at least some of the decisions taken by Tikader and Bastawade (1983) must be viewed with suspicion. For example, they rejected Couzijn's (1981) synonymy of *Palamnaeus fulvipes madraspatensis* Pocock, 1900 with *H. fulvipes*, instead elevating the subspecies to the rank of species. The redescription by Tikader and Bastawade of *H. madraspatensis* was based on two adult ♂, whereas their redescription of *H. fulvipes* was based on an adult ♀. During the course of the present investigation, the type specimens of *P. fulvipes madraspatensis* (previously examined by Tikader and Bastawade) were re-examined and compared with specimens of *H. fulvipes*, including some from the type locality of *P. fulvipes madraspatensis*. On the basis of this comparison there is no doubt that *P. fulvipes madraspatensis* is conspecific with *H. fulvipes*. This is a yet another example where the adults of a sexually dimorphic species of scorpion have been classified as different species, a conclusion also reached by Couzijn (1981: 135–136), who stated: 'The subspecies *P. fulvipes madraspatensis* … [does] not show other differences from *B. fulvipes* Koch than the … ratio of length and width of the male's pedipalp hand'.

The small sample size of specimens examined by Tikader and Bastawade (usually one or two at most) and the propensity for marked sexual dimorphism in many species of *Heterometrus*, as in *Opistophthalmus* (Prendini 2001*e*), suggests that many of the synonyms resurrected and subspecies elevated by those authors may be synonymous with one another or with existing species. That said, Couzijn's approach of retaining numerous subspecies within widespread species is equally inadequate. Clearly, the genus *Heterometrus* represents another scorpionid radiation, smaller than, but similar in several respects to, the *Opistophthalmus* radiation in southern Africa (see below). Numerous range-restricted or narrowly endemic species and species-complexes can therefore be expected in the genus. Simply partitioning the morphological variation into a few widespread polymorphic species with many subspecies (e.g. Couzijn 1981) will not alleviate the taxonomic problems. Obviously, subspecies cannot be elevated on the basis of one or a few specimens (e.g. Tikader and Bastawade 1983) either. A thorough revision, involving the examination of many specimens, in order to determine which characters are consistent across the range of the various taxa, is required. Subspecies that can be consistently differentiated from other subspecies by means of a diagnostic character combination should be elevated to the rank of species. If they cannot be consistently differentiated, then they should be synonymised. Molecular data (e.g. DNA sequences) may also help to clarify species limits within *Heterometrus*, as has been found in other complex scorpion genera (Newlands 1980; Newlands and Cantrell 1985; Gantenbein and Scholl 1998; Gantenbein *et al.* 1999*a*, 1999*b*, 2000*a*, 2000*b*, 2001*a*, 2001*b*; Scherabon *et al.* 2000; Fet *et al.* 2001). Finally, a computational cladistic analysis of relationships among the species of *Heterometrus* remains to be presented—Couzijn's (1981: 181–182, fig. 66) cladogram was constructed manually. This should help to clarify the validity of the five subgenera currently recognised.

Diagnosis

Heterometrus is the sister-genus of *Pandinus* (Prendini 2000*a*). Both species share the following characters, by which they can be separated from *Opistophthalmus* and *Scorpio*: presence of a stridulatory organ, comprising a 'rasp' (granular tubercles) and 'scraper' (stridulatory setae or scaphotrix), on opposing surfaces of the coxae of the

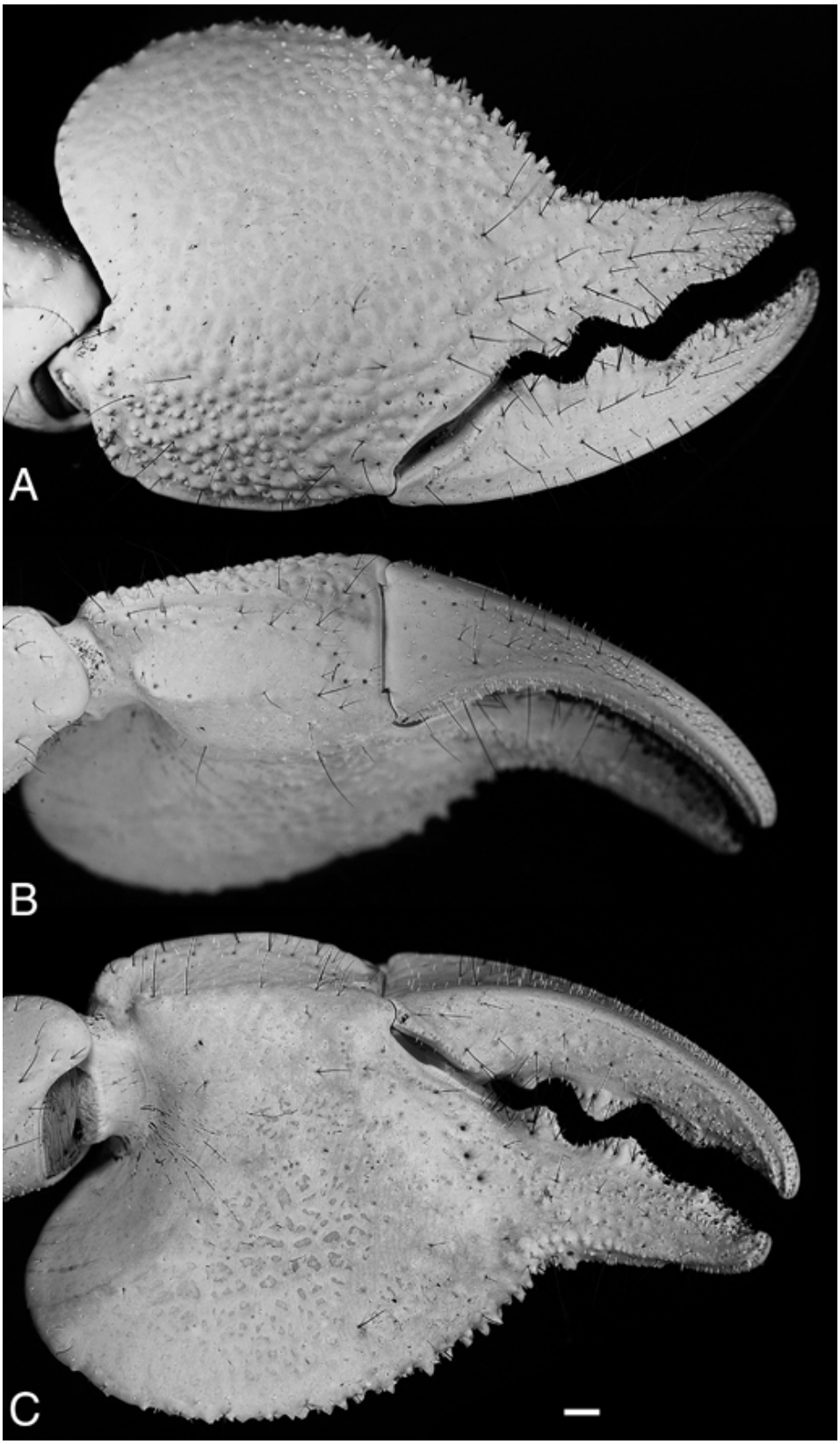

Fig. 13. Dextral pedipalp chela of *Pandinus imperator* (C. L. Koch, 1841), ♂ (AMNH), illustrating trichobothria, macrosetae and surface macrosculpture in dorsoexternal (*A*), ventral (*B*) and internal (*C*) aspects. Scale bar = 1 mm.

pedipalps and the first pair of legs; equal counts of ventrosubmedian spiniform macrosetae on telotarsi I–II and III–IV. *Heterometrus* can be separated from *Pandinus* by the following characters: pedipalps orthobothriotaxic, with 26 trichobothria (patella with 13 trichobothria in *e* series and 3 trichobothria in *v* series; chela with 4 trichobothria in *V* series and 2 trichobothria in *i* series); granular tubercles of 'rasp' and stridulatory setae (scaphotrix) of 'scraper' situated on coxae of first leg and pedipalp, respectively. *Heterometrus* can be further separated from *Opistophthalmus* by the following characters: pedipalps orthobothriotaxic, with 26 trichobothria (including 13 trichobothria in *e* series of patella); cheliceral coxae without stridulatory setae (scaphotrix) on dorsointernal surfaces and chemoreceptive lamelliform setae (trichocopae) on internomedian surfaces. *Heterometrus* can be further separated from *Scorpio* by the following characters: digital carina of pedipalp chela obsolete; sternite VII without paired ventrosubmedian and ventrolateral carinae.

Description

The following account updates and enlarges on the detailed description provided by Couzijn (1981). Characters that are invariant within the Scorpionidae are omitted.

Colour. Entirely dark brown or black (with or without pale legs and telson).

Carapace. Median notch in anterior margin present, deep (Fig. 9*A*); rostrolateral margin often with a distinct notch next to posterior lateral ocelli. Median longitudinal sulcus narrow, suturiform, with or without a distinct anterior furcation; anteromedian and anterocular depressions absent. Posterior carapacial sutures present but may be indistinct. Three pairs of lateral ocelli. Median ocular tubercle raised, situated medially; superciliary carinae higher than ocelli, usually extended anteriorly and often also posteriorly. Surfaces of carapace finely to coarsely granular laterally, smooth to coarsely granular in interocular region, and smooth posteromedially (♂, ♀).

Chelicerae. Movable finger with distal external and distal internal teeth not opposable to moderately opposable (Fig. 10*A*, *B*). Cheliceral coxae without stridulatory setae (scaphotrix) on dorsointernal surfaces and chemoreceptive lamelliform setae (trichocopae) on internomedian surfaces.

Pedipalps. Chela surface macrosculpture varying from smooth or reticulate to coarsely granular. Chela dorsal secondary, subdigital, digital and ventromedian carinae obsolete (Fig. 11). Chela fingers granular; second lobe of movable finger (♂) often more strongly developed than other lobes, with correspondingly well-developed notch in fixed finger; externodistal edge of fixed finger with deep notch for terminal denticle of movable finger.

Patella with anterior process obsolete and dorsal surface convex, dorsomedian carina raised above horizontal axis of dorsoexternal carina; dorsomedian, ventroexternal and paired externomedian carinae obsolete to absent (Fig. 15*A–C*); dorsoexternal and internomedian carinae obsolete, moderately or well developed. Internomedian carina often comprising several enlarged spiniform granules.

Femur dorsoexternal carina present and more strongly developed than dorsointernal carina; internomedian carina oriented diagonally between ventrointernal and dorsointernal carinae; ventroexternal and ventroexternal secondary carinae absent.

Trichobothria. Pedipalps type C orthobothriotaxic (Figs 11, 15*A–C*), with 26 trichobothria (patella with 13 trichobothria in *e* series and 3 trichobothria in *v* series; chela with 4 trichobothria in *V* series and 2 trichobothria in *i* series). Femur with trichobothrium *i* located on dorsal surface.

Pectines. Internal fulcral plates smooth proximally but densely setose (microsetae only) distally. First proximal median lamella of each pecten with mesial margin angular and pectinal teeth present along entire posterior margin. Pectinal teeth (♂) straight and elongate.

Genital operculum. Genital opercula (♂) usually overlapping partially.

Legs. First pair of maxillary lobes (coxapophyses) usually tapering anteriorly, longer than, and encircling second pair. Stridulatory organs, comprising a 'rasp' (granular tubercles) and 'scraper' (stridulatory setae or scaphotrix), present on opposing surfaces of coxae of first leg (Fig. 17*B*) and pedipalp (Fig. 17*A*), respectively. Femora each with paired carinae on prolateral surface. Basitarsi I and II each with a retrolateral row of spiniform macrosetae, but tibiae I and II usually without a retrolateral row of spiniform macrosetae. Telotarsi I–IV short, stout and distally broadened in dorsal and lateral views, with dorsomedian lobe approximately equal to laterodistal lobes; telotarsi each with paired ventrosubmedian rows of spiniform macrosetae, two of which are inserted on laterodistal lobes; counts of ventrosubmedian spiniform macrosetae equal on telotarsi I–II and III–IV (Fig. 19*A–D*).

Mesosoma. Post-tergites smooth medially and coarsely granular laterally, to entirely smooth. Sternites smooth (Fig. 21*A*). Sternite VII usually acarinate or with a pair of obsolete ventrolateral carinae.

Metasoma and telson. Metasomal segments I–IV each with paired ventrosubmedian and ventrolateral carinae, equally developed on all segments (Fig. 21*A*); intercarinal surfaces sparsely granular, except for ventral surfaces of segments I–III, which are smooth (♂, ♀). Segment V smooth or granular dorsally, granular ventrally; ventrolateral carinae comprising spiniform denticles; distal portion of ventromedian carina continuous. Telson vesicle granular ventrally, smooth laterally.

Male reproductive anatomy. Hemispermatophore with distal lamina truncate distally and an accessory distal lobe protruding between articular suture and distal lobe (hook).

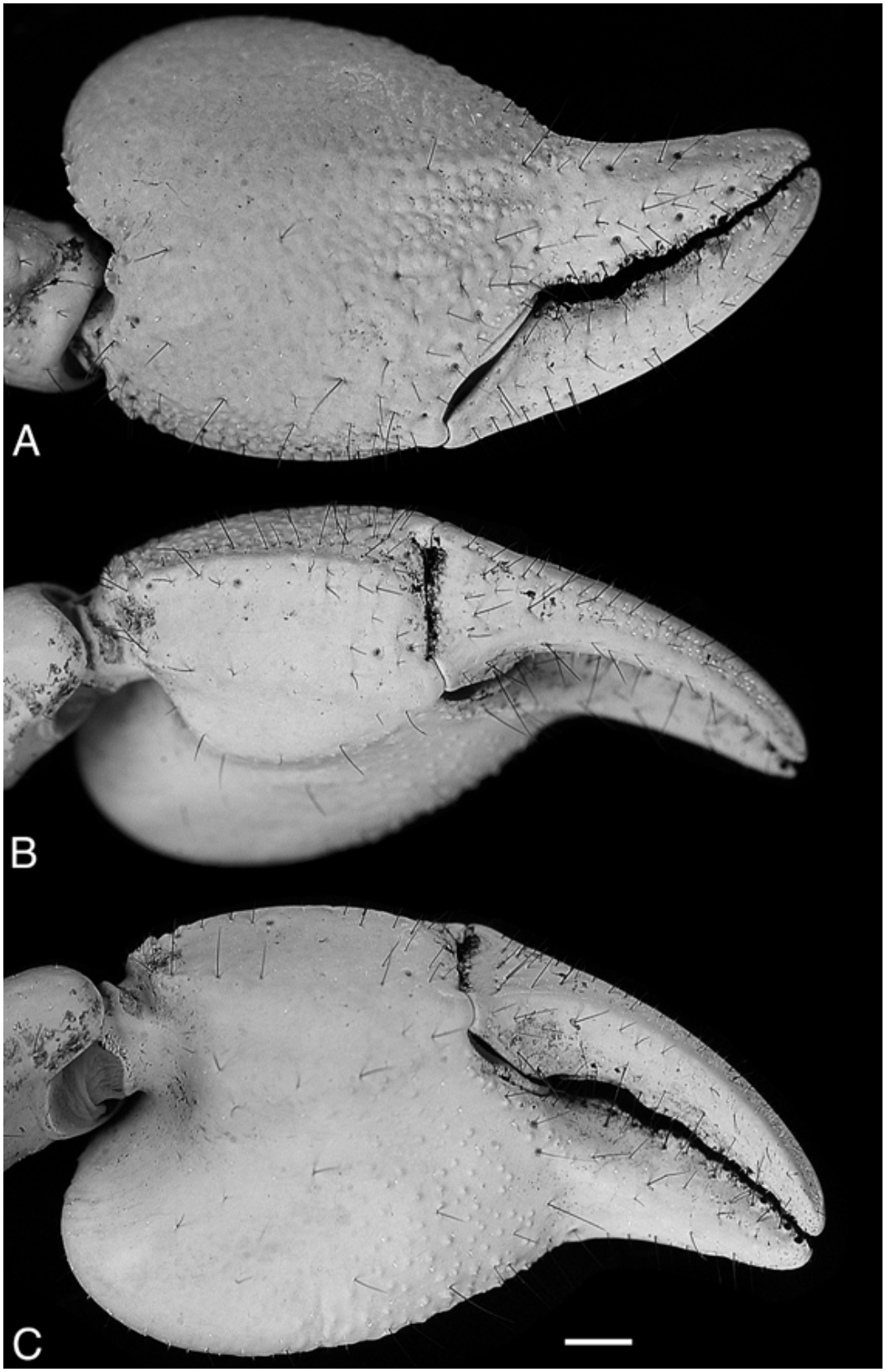

Fig. 14. Dextral pedipalp chela of *Scorpio maurus palmatus* (Ehrenberg, 1828), ♀ (AMNH), illustrating trichobothria, macrosetae and surface macrosculpture in dorsoexternal (*A*), ventral (*B*) and internal (*C*) aspects. Scale bar = 1 mm.

Included taxa

Heterometrus currently includes 30 species and 27 subspecies, including eight nominotypical forms, placed into five subgenera (Couzijn 1981; Tikader and Bastawade 1983; Fet 2000): *Chersonesometrus* Couzijn, 1978; *Gigantometrus* Couzijn, 1978; *Heterometrus* Ehrenberg, 1828; *Javanimetrus* Couzijn, 1981; and *Srilankametrus* Couzijn, 1981.

Ecology

The ability to construct burrows has been confirmed in at least four of the Indian species: *H. fulvipes*, *H. indus* (DeGeer, 1778), *H. swammerdami* and *H. xanthopus* (Pocock, 1897) (Khatavkar and More 1990; Hull-Williams 1989; Shivashankar and Veeresh 1991; Shivashankar 1992; Tare *et al.* 1993), and one South-East Asian species, *H. cyaneus* (C. L. Koch, 1836) (Couzijn 1981). Burrows are constructed in loamy riverbanks and other sloping ground, at the base of stones and among the roots of trees (Couzijn 1981; Shivashankar 1994). As in some species of *Pandinus*, composite, multi-entranced burrows containing multiple (up to 15) related individuals of different ages have been recorded in some species, such as *H. fulvipes* (Shivashankar 1994). In others, such as *H. longimanus* (Herbst, 1800) and *H. spinifer*, mixed age groups of related and unrelated individuals cohabit with minimal aggression or cannibalism in laboratory terraria (Harrison 1954; Polis and Lourenço 1986) and, according to some evidence, this also occurs in the wild (Schultze 1927).

Ecological data are unavailable for the remaining species of *Heterometrus*. However, the thickened metasoma, short, robust legs with stout, spiniform macrosetae distributed laterally and distally on the basitarsi, and curved telotarsal ungues of the Indian and Sri Lankan species are indicative of a fossorial, and essentially pelophilous, habit, as recorded for the burrowing species listed above. It is presently unclear as to whether burrowing occurs in most of the South-East Asian species, or may have been secondarily lost. For example, Schultze (1927) notes that *H. longimanus* occurs under the loose bark of dead standing trees, under decaying trunks and logs, or in the cavities of rotten tree stumps, but makes no mention of burrows. Furthermore, the morphology of most of the South-East Asian species differs from the Indian and Sri Lankan species in the absence of a retrolateral row of spiniform macrosetae on the tibia, in the presence of strongly curved telotarsal ungues and, in many species (e.g. *H. laoticus*) an enlarged, curved pseudonychium (dactyl). Although such features are uncommon among the scorpionids, they occur in arboreal chactids (e.g. *Chactas* Gervais, 1844) and ischnurids (e.g. *Liocheles* Sundevall, 1833 and some species of *Opisthacanthus* Peters, 1861), and are regarded as corticolous adaptations to an arboreal habitat (Prendini 2001*f*). No species of *Heterometrus* exhibits psammophilous or lithophilous adaptations.

Distribution

Asia: Bangladesh, Bhutan, Brunei, Cambodia, India (including Lesser Nikobar Islands), Indonesia (Babi, Bangka, Batu, Belitung, Bengkalis, Java, Kalimantan, Madura, Mentawei, Nias, Riau Islands, Sulu Islands, Sumatra, Weh), Laos, Malaysia (mainland and Sarawak), Myanmar, Nepal, Philippines (Balabac, Luzon, Mindanao, Palawan), Singapore, Sri Lanka, Thailand, Vietnam.

Species of the genus are distributed from India and Sri Lanka throughout the South-East Asian mainland and archipelagos as far as Wallace's Line, where they inhabit tropical and subtropical rainforests, moist and dry tropical deciduous forests, and tropical thorn forests (Couzijn 1981; Tikader and Bastawade 1983; Sissom 1990). According to Couzijn (1981: 175, 178) there is an unconfirmed record of *H. longimanus* from the Sula Islands, in the Moluccas across Wallace's Line. However, this may also refer to the Sulu archipelago between north-eastern Borneo and Mindanao, where a subspecies of *H. longimanus* has been recorded. Until this record has been confirmed, the distribution of *Heterometrus* should be regarded as bordered by Wallace's Line, following previous authors (Vachon 1953; Couzijn 1981).

Conservation status

As is the case with *Pandinus* (discussed below), several species of *Heterometrus* are readily available in Europe, the USA and Japan for the exotic pet trade. Their impressive size and fearsome appearance are highly prized by collectors. An extensive literature on the captive husbandry of these so-called 'Asian forest scorpions' exists (e.g. Nemenz and Gruber 1967; Hull-Williams 1986; Hosoi 1990; Dupré 1993; Gopalakrischnakone *et al.* 1995; Condevaux-Lanloy 1996; Mahsberg *et al.* 1999; Rubio 2000). The following species and alleged countries of origin have been personally recorded in the trade: *H. cyaneus* (Java, Indonesia); *H. fulvipes* (India); *H. laoticus* (Vietnam); *H. longimanus* ('Burma'); *H. spinifer* (Thailand); *H. swammerdami* (India). Owing to the difficulties involved in the identification of *Heterometrus* species, especially those occurring in South-East Asia (Dupré 1989), species are often advertised under false or erroneous names.

In addition to being sold alive as pets, many South-East Asian *Heterometrus* are dried and mounted in glass cases or set in resin to be sold as curios. Both *H. laoticus* and *H. spinifer* have been observed by us for sale as curios in the USA, UK, Thailand, Singapore and South Africa.

Unfortunately, as with *Pandinus*, wild populations of *Heterometrus* species are expected to be slow to repopulate after harvesting for the following reasons. Females have gestation periods up to 12 months (Subburam and Reddy 1978) and produce fairly small broods (30–35) compared with other scorpions (Schultze 1927; Mathew 1956; Polis and

Sissom 1990; Shivashankar 1994; Condevaux-Lanloy 1996). Young are relatively altricial, spending several months in the maternal burrow before dispersing (Schultze 1927; Shivashankar 1994), thereby further protracting the period before a female can give birth to her next brood. Age to sexual maturity is 4–7 years in these scorpions (Polis and Lourenço 1986; Polis and Sissom 1990), during which most juveniles experience natural predation (including cannibalism).

These factors suggest that species of *Heterometrus* are extremely vulnerable to overharvesting and, unlike *Pandinus*, three species of which receive protection from CITES (the Convention on International Trade on Endangered Species) (IUCN 1994; Lourenço and Cloudsley-Thompson 1996), no species of *Heterometrus* is currently listed by CITES. The apparently restricted distributions of many species provide further cause for concern, especially given that the remaining wild populations are threatened not only by overexploitation but also by continued habitat destruction (e.g. through deforestation). *Heterometrus* species appear to be restricted to virgin habitat (e.g. Schultze 1927) and may thus be regarded as equilibrium species. Another threat to the survival of many *Heterometrus* species in South-East Asia is posed by the local inhabitants, for whom these scorpions represent a common ingredient in the daily diet (Menzel and D'Aluisio 1998).

Genus ***Opistophthalmus*** C. L. Koch

Opistophthalmus C. L. Koch, 1837: 36, 37; Simon, 1880: 391, 392; Francke, 1985: 3; Lourenço, 1989: 174; Sissom, 1990: 131; Fet, 2000: 448, 449; Lourenço, 2000: 25; Prendini, 2000*a*: 44. Type species, by original designation: *Scorpio capensis* Herbst, 1800 [= *Opistophthalmus capensis* (Herbst, 1800)].

Atreus C. L. Koch, 1837 : pl. VI, fig. 66[5].

Opisthophthalmus: Peters, 1861: 512; Thorell, 1876*a*: 13; 1876*b*: 84; Karsch, 1879*a*: 20; Kraepelin, 1894: 77; Laurie, 1896*a*: 193; 1896*b*: 128; Lönnberg, 1897: 197; Purcell, 1898: 1; 1899: 10; Kraepelin, 1899: 125; 1913: 185; Birula ,1917*a*: 161; 1917*b*: 59; Werner, 1934: 278; Kästner, 1941: 234; Bücherl, 1964: 59; Lamoral, 1979: 668, 670; Nenilin & Fet, 1992: 15, 16; Kovařík 1998: 138[6].

Miaephonus Thorell, 1876*a*: 13; 1876*b*: 84; Karsch, 1879*a*: 20; Laurie, 1896*b*: 128. Type species, by original designation: *Miaephonus wahlbergii* Thorell, 1876 [= *Opistophthalmus wahlbergii* (Thorell, 1876)]. Synonymised: Kraepelin, 1894: 77.

Petrooicus Karsch, 1879*b*: 109, 110. Type species, by original designation: *Petrooicus carinatus* (Peters, 1861) [= *Opistophthalmus carinatus* (Peters, 1861)]. Synonymised: Pocock, 1893: 307.

Petrovicus: Simon, 1888: 380, 381.

Mossamedes Simon, 1888: 381, 382. Type species, by monotypy: *Mossamedes opinatus* Simon, 1888 [= *Opistophthalmus opinatus* (Simon, 1888)]. Synonymised: Pocock, 1893: 307.

Oecopetrus Pocock, 1893: 307; Laurie, 1896*b*: 128. Synonymised: Kraepelin, 1899: 125[7].

Protophthalmus Lawrence, 1969: 105; Lamoral, 1972: 118, 119; Lamoral & Reynders, 1975: 569. Type species: *Protophthalmus holmi* Lawrence, 1969. Synonymised: Newlands, 1972*a*: 241.

Opistophthalmus is the most speciose and most morphologically diverse genus of the Scorpionidae. Compared with the other scorpionid genera, this genus is characterised by numerous morphological apomorphies, many of which are also unique among scorpions. For example, most species of the genus possess organs for chemoreception and stridulation on the chelicerae (Pocock 1896*b*; Purcell 1899; Hewitt 1915, 1918, 1925, 1931; Skaife 1920; Pavlovsky 1924*a*; Lawrence 1928, 1971, 1973; Werner 1934; Millot and Vachon 1949; Alexander and Ewer 1957; Alexander 1958, 1959; Vachon *et al.* 1958, 1960; Dumortier 1964; Sissom 1990; Prendini 2000*a*). A unique proximal displacement of the median ocelli on the carapace (Hewitt 1925; Lawrence 1969; Newlands 1972*a*, 1978), from which the genus derives its Latin name (Skaife 1920, 1954), is exhibited by many species. Most species also display peculiar, segmentally variable surface macrosculpture of the mesosomal sternites and ventral side of the first four metasomal segments, often associated with loss or reduction of the ventrosubmedian and ventrolateral metasomal carinae (Hewitt 1918, 1925; Prendini 2000*b*).

Among other characters, some species of *Opistophthalmus* display exceptionally high pedipalp trichobothrial counts among scorpions, whereas others display exceptionally low pectinal tooth counts, including the lowest count of any known scorpion in a species to be described in a forthcoming revision (L. Prendini, unpublished data). The genus is further characterised by marked extremes in adult size, varying from among the largest known scorpion species, such as *O. gigas* Purcell, 1898, which commonly reaches 160 mm in length, to dwarves (including the smallest scorpionid species) such as *O. pygmaeus* Lamoral, 1979, a mere 40 mm long. All members of the genus are also characterised by ecomorphological specialisations to substrata of specific hardness and composition (Newlands 1972*a*, 1972*b*; Eastwood 1978*b*; Lamoral 1979; Prendini 2001*f*). Finally, most species in the genus display exaggerated sexual dimorphism in the shape of the pedipalp chelae (Purcell 1899; Hewitt 1918, 1925; Newlands 1972*a*; Eastwood 1978*b*; Prendini 2000*b*), surface macrosculpture of the pedipalps, mesosoma and metasoma, and the pectinal tooth counts (Hewitt 1925; Lawrence 1969; Newlands 1972*a*; Lamoral 1979).

Diagnosis

Opistophthalmus is the most basal genus of the Scorpionidae, forming the sister-group of the monophyletic group comprising (*Scorpio* (*Heterometrus* + *Pandinus*)). Most species of the genus can be separated from *Heterometrus*, *Pandinus* and *Scorpio* by the following characters: cheliceral coxae with stridulatory setae (scaphotrix) on dorsointernal surfaces and with chemoreceptive lamelliform setae (trichocopae) on internomedian surfaces. *Opistophthalmus* can be further separated from *Heterometrus* and *Pandinus* by the following

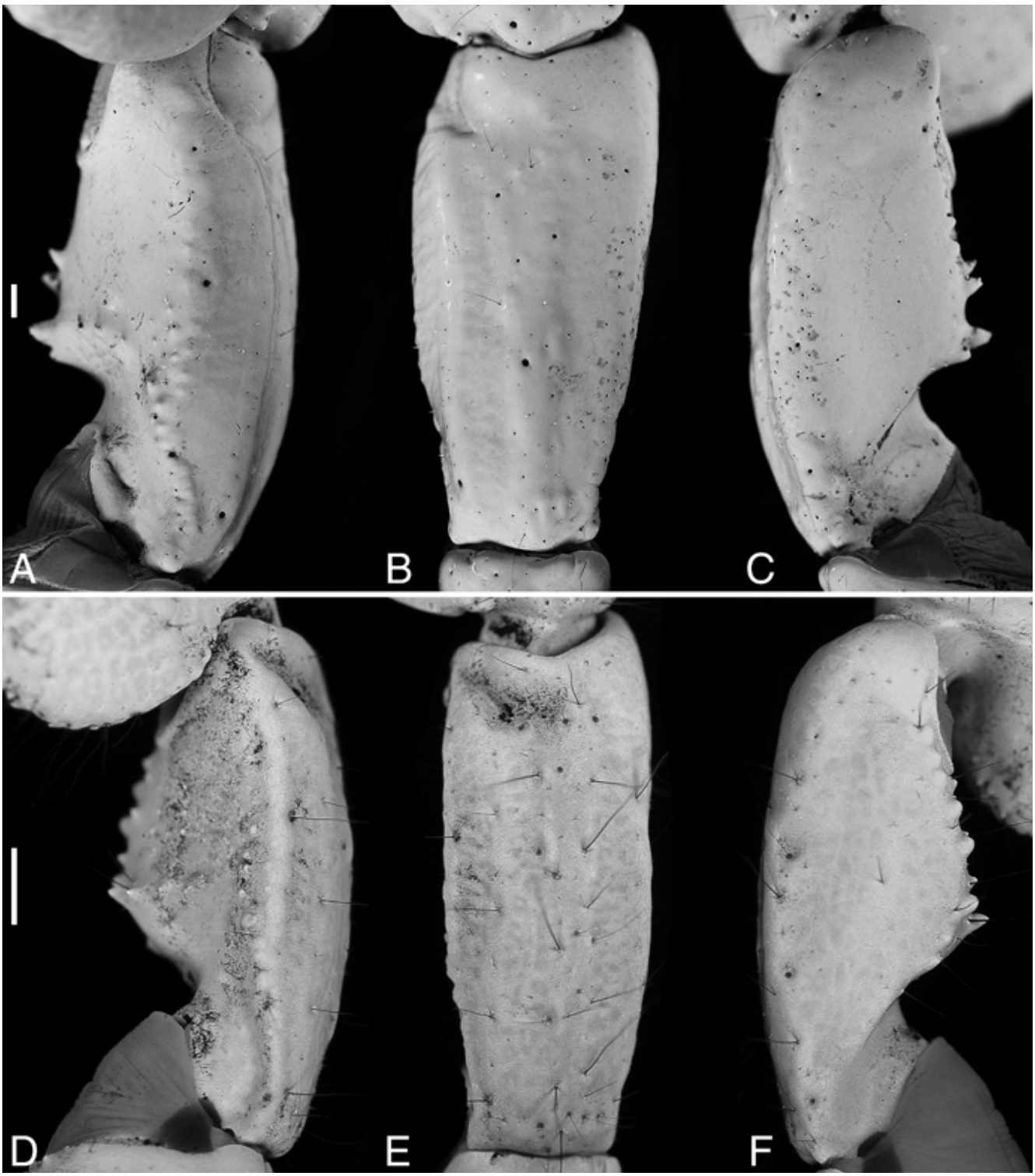

Fig. 15. Dextral pedipalp patella of representative scorpionids, illustrating trichobothria, macrosetae and surface macrosculpture in dorsal (*A*, *D*), external (*B*, *E*) and ventral aspects (*C*, *F*). *A*, *C*, *Heterometrus spinifer* (Ehrenberg, 1828), ♀ (AMNH). *D*, *F*, *Opistophthalmus capensis* (Herbst, 1800), ♂ (AMNH). Scale bars = 1 mm.

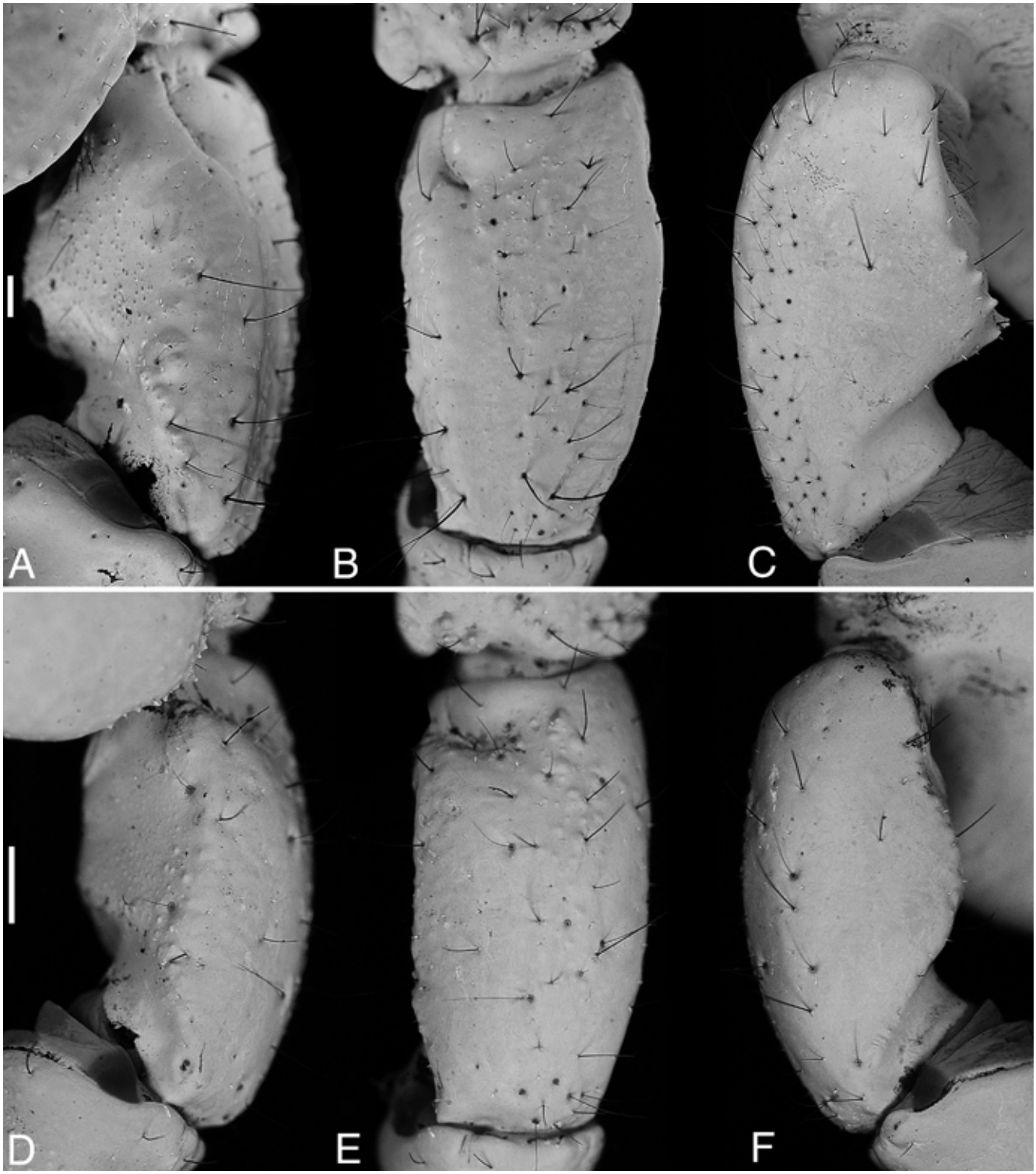

Fig. 16. Dextral pedipalp patella of representative scorpionids, illustrating trichobothria, macrosetae and surface macrosculpture in dorsal (*A*, *D*), external (*B*, *E*) and ventral aspects (*C*, *F*). *A*, *C*, *Pandinus imperator* (C. L. Koch, 1841), ♂ (AMNH). *D*, *F*, *Scorpio maurus palmatus* (Ehrenberg, 1828), ♀ (AMNH). Scale bars = 1 mm.

characters: absence of a stridulatory organ, comprising a 'rasp' (granular tubercles) and 'scraper' (stridulatory setae or scaphotrix), on opposing surfaces of the coxae of the pedipalps and the first pair of legs; digital carina of pedipalp chela distinct; counts of ventrosubmedian spiniform macrosetae increasing from telotarsi I–II to III–IV. *Opistophthalmus* can be further separated from *Heterometrus* and *Scorpio* by the following character: pedipalps neobothriotaxic major, with more than 26 trichobothria (including more than 13 trichobothria in *e* series of patella).

Description

Besides the brief diagnosis provided by Lamoral (1979), a formal description of this genus has not been presented since Kraepelin (1899). The following account updates and enlarges on the latter. Characters that are invariant within the Scorpionidae are omitted.

Colour. Varies from entirely dark brown or black (with or without pale legs and telson) to entirely pale, with combinations of dark tergites (with or without dark sternites and metasoma), pale legs and pale carapace and/or pedipalps in many species. Telson often similar to or darker than metasoma.

Carapace. Median notch in anterior margin shallow (Fig. 9*B*) or absent; rostrolateral margin entire. Median longitudinal sulcus narrow, suturiform, often with anterior furcation, but sutures may be weakly developed or absent; anteromedian and anterocular depressions may be present. Posterior carapacial sutures present or absent. Usually three but rarely two pairs of lateral ocelli. Median ocular tubercle raised or shallow, situated medially, posteromedially or extremely posteriorly (rarely anteromedially); superciliary carinae higher or lower than ocelli, occasionally extended anteriorly but never posteriorly. Surfaces of carapace finely to very coarsely granular laterally, smooth, finely or coarsely granular in interocular region, and smooth, finely or coarsely granular posteromedially (♂, ♀).

Chelicerae. Movable finger with distal external and distal internal teeth not opposable (Fig. 10*C*, *D*) or moderately opposable. Cheliceral coxae usually with stridulatory setae (scaphotrix) on dorsointernal surfaces (Fig. 10*D*) and chemoreceptive lamelliform setae (trichocopae) on internomedian surfaces (Fig. 10*C*, *D*; one or both may be present).

Patella usually with dorsal surface convex, dorsomedian carina raised above horizontal axis of dorsoexternal carina, and with anterior process obsolete (Fig. 15*D*, *E*), less often with dorsal surface flat, dorsomedian and dorsoexternal carina in same axis, and/or with anterior process moderately developed; dorsomedian carina usually distinct but occasionally obsolete; dorsoexternal and internomedian carinae obsolete, moderately or well developed; ventroexternal and paired externomedian carinae usually distinct, less often obsolete (Fig. 15*E*, *F*). If distinct, internomedian carina may comprise several enlarged spiniform granules.

Pedipalps. Chela surface macrosculpture varying from smooth or reticulate to finely or coarsely granular. Chela dorsal secondary and subdigital carinae distinct or obsolete; digital and ventromedian carinae usually distinct (Fig. 12) but occasionally obsolete. Chela fingers usually smooth (rarely granular); second lobe of movable finger (♂) occasionally larger and more strongly developed than other lobes, with correspondingly well-developed notch in fixed finger, but usually not larger than other lobes; externodistal edge of fixed finger with shallow notch for terminal denticle of movable finger.

Femur dorsoexternal carina less strongly developed than dorsointernal carina; internomedian carina usually oriented diagonally between ventrointernal and dorsointernal carinae, less often oriented parallel to dorsointernal and ventrointernal carinae; ventroexternal and ventroexternal secondary carinae usually present, less often absent.

Trichobothria. Pedipalps type C neobothriotaxic major (Figs 12, 15*D–F*), with more than 26 trichobothria (patella with more than 13 trichobothria in *e* series and often more than 3 trichobothria in *v* series; chela rarely with more than 4 trichobothria in *V* series). Femur with trichobothrium *i* located on dorsal surface.

Pectines. Internal fulcral plates sparsely setose (macrosetae scattered over entire surface). First proximal median lamella of each pecten with mesial margin angular and pectinal teeth present along entire posterior margin or with mesial margin shallowly curved and proximal region of posterior margin devoid of teeth. Pectinal teeth (♂) straight and elongate or short and curved.

Genital operculum. Genital opercula (♂) not overlapping.

Legs. First pair of maxillary lobes (coxapophyses) usually rounded–truncate anteriorly and roughly equal in length to second pair (but tapering anteriorly, longer than, and encircling second pair in some). Stridulatory organs, comprising a 'rasp' (granular tubercles) and 'scraper' (stridulatory setae or scaphotrix), absent from opposing surfaces of coxae of pedipalps and first pair of legs (Fig. 17*C*, *D*). Femora each with a single carina on prolateral surface. Tibiae I and II and basitarsi I and II each with one or more retrolateral rows of spiniform or setiform macrosetae (Fig. 19*E*, *F*). Telotarsi I–IV long, narrow, parallel sided in dorsal and lateral views, with dorsomedian lobe considerably shorter than laterodistal lobes or short, stout and distally broadened in dorsal and lateral views, with dorsomedian lobe approximately equal to laterodistal lobes; telotarsi each with paired ventrosubmedian rows of spiniform macrosetae (prolateral row often absent), four or five of which are inserted on laterodistal lobes (Fig. 19*E–H*); counts of

ventrosubmedian spiniform macrosetae increasing from telotarsi I–II to III–IV.

Mesosoma. Post-tergites smooth medially and finely or coarsely granular laterally, to entirely smooth (♀); smooth medially and finely or coarsely granular laterally, to entirely finely or coarsely granular (♂). Sternites smooth (♂, ♀), III–VII rugose (♂ only), or III–VII or VII only, granular or tuberculate (♂ and, more rarely, ♀; Fig. 21*B*). Sternite VII usually acarinate or with a pair of obsolete ventrolateral carinae, but with four strongly developed carinae (paired ventrosubmedian and ventrolateral) in *O. boehmi*.

Metasoma and telson. Metasomal segments I–IV each with paired ventrosubmedian and ventrolateral carinae, usually more strongly developed on segments III and IV but often obsolete or absent on one or all segments (Fig. 21*B*), and more strongly developed on segments I and II in *O. boehmi*; intercarinal surfaces usually sparsely granular, except for ventral surfaces of segments I–III and occasionally IV, which may be granular or smooth (♂, ♀), rugose (♂ only) or tuberculate (♂ and, more rarely, ♀). Segment V smooth or granular dorsally, granular ventrally; ventrolateral carinae comprising rounded granules or spiniform denticles, and with distal portion of ventromedian carina continuous, weakly bifurcating or breaking up into numerous granules (*O. boehmi* only). Telson vesicle granular ventrally and, occasionally, laterally (spicules also present), to entirely smooth.

Male reproductive anatomy. Hemispermatophore with distal lamina truncate distally (or rarely tapering), without an accessory distal lobe protruding between articular suture and distal lobe (hook).

Included taxa

As shall be presented in a forthcoming revision (L. Prendini, unpublished data), the genus comprises approximately 80 species and is therefore the second largest scorpion genus, after the Neotropical buthid genus *Tityus* C. L. Koch, 1836. No subgenera are to be recognised, but the species will be assigned to several informal species-groups.

Ecology

All species of *Opistophthalmus* are obligate burrowers, constructing burrows under stones or in open ground (Purcell 1899; Skaife 1920; Lawrence 1971, 1973; Newlands 1972*a*, 1972*b*, 1978; Eastwood 1978*a*, 1978*b*; Lamoral 1978*a*, 1979). As in *Scorpio*, most *Opistophthalmus* are highly cannibalistic, hence cohabitation of multiple individuals within a single burrow (except during courtship or parental care) and the communal construction of burrows are absent (Eastwood 1978*a*, 1978*b*). Burrows vary from shallow scrapes to elaborate, spiralling tunnels reaching depths of more than 1 m below the surface, depending on the species. Each species constructs burrows in substrata of specific hardness and composition, varying from unconsolidated sand dunes to compacted clayey soils, depending on the species (Newlands 1972*a*, 1972*b*, 1978; Lamoral 1978*a*, 1979). Several species have adapted to extremely rocky habitats (e.g. scree slopes) and virtually lost the ability to burrow, sheltering under stones instead (Purcell 1899; Hewitt 1925; Eastwood 1978*b*). The ability of different species to burrow in substrata of specific hardness correlates closely with their morphology, such that a gradation of ecomorphotypes can be recognised, from lithophilous through pelophilous to psammophilous (Newlands 1972*a*, 1972*b*, 1978; Lamoral 1979; Prendini 2001*f*).

Distribution

Africa: Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Tanzania, Zambia, Zimbabwe.

Opistophthalmus is distributed from the Cape Peninsula of South Africa to Mount Kilimanjaro in Tanzania. The genus is absent from the tropical rainforests of the Congo basin and no records are known from north of the equator. It is not known whether the Tanzanian population of *O. boehmi* extends into southern Kenya, but records of this species from the Kilimanjaro area, just south of the Kenyan border, suggest that this may be the case. Dupré (1992) cites imported specimens of *O. boehmi* as originating from Kenya, but this also remains unconfirmed.

Conservation status

Habitat destruction through agriculture (ploughing), deforestation and urbanisation poses the greatest threat to species of *Opistophthalmus*, most of which are ecologically specialised (thus only occurring in pristine habitat), and extremely range restricted. At least one species appears to be extinct, while several others are critically endangered, particularly in the Western Cape province of South Africa (Prendini 2001*d*).

The international trade in exotic pets poses a small but ever-increasing threat to the future survival of *Opistophthalmus* species, given their increasing popularity as pets on the one hand, and their extremely restricted distributions, together with the continued destruction of their habitat, on the other. Two species, *O. glabrifrons* (the 'yellow-legged' or 'shiny burrowing scorpion') and *O. wahlbergii* ('Wahlberg's tri-coloured scorpion'), allegedly imported from Mozambique, are commonly available in Europe, the USA and Japan. Given that the distribution of *O. wahlbergii* does not extend to Mozambique, and that the form offered occurs only in eastern Botswana, southern Zimbabwe and the Northern Province of South Africa, these scorpions are probably illegally collected and exported from one of the latter countries. A third species, *O. boehmi*, which has been advertised as the 'tri-coloured scorpion' in the USA (personal observation) and as the 'Kilimanjaro mustard scorpion' in Japan (K. Suzusaki, personal communication),

is occasionally imported from Tanzania and perhaps Kenya (Dupré 1992), although its occurrence in Kenya remains unconfirmed. More often, female specimens of *P. cavimanus*, which also occurs in Kenya and Tanzania, are mistakenly advertised as *O. boehmi* (personal observation). Specimens of the southern population of *O. boehmi*, which occurs in western Mozambique, southern Zimbabwe, the Northern Province of South Africa and north-eastern Botswana, have also appeared occasionally in the pet trade (photographs and specimens supplied by R. D. Gaban, personal communication).

The increasing appearance of such species and others, for example *O. carinatus* (pictures of an endemic Namibian colour form of which were recently posted on a prominent website for scorpion enthusiasts), in international collections is a matter of concern, given the frequency with which invertebrates are being smuggled illegally, along with insects and reptiles, out of southern African countries (A. L. de Villers, K. de Wet, M. Forsyth, P. Geldenhuys, A. Leroy and R. Stals, personal communications). The presence in the international pet trade of scorpions that originated from South Africa has always been difficult to

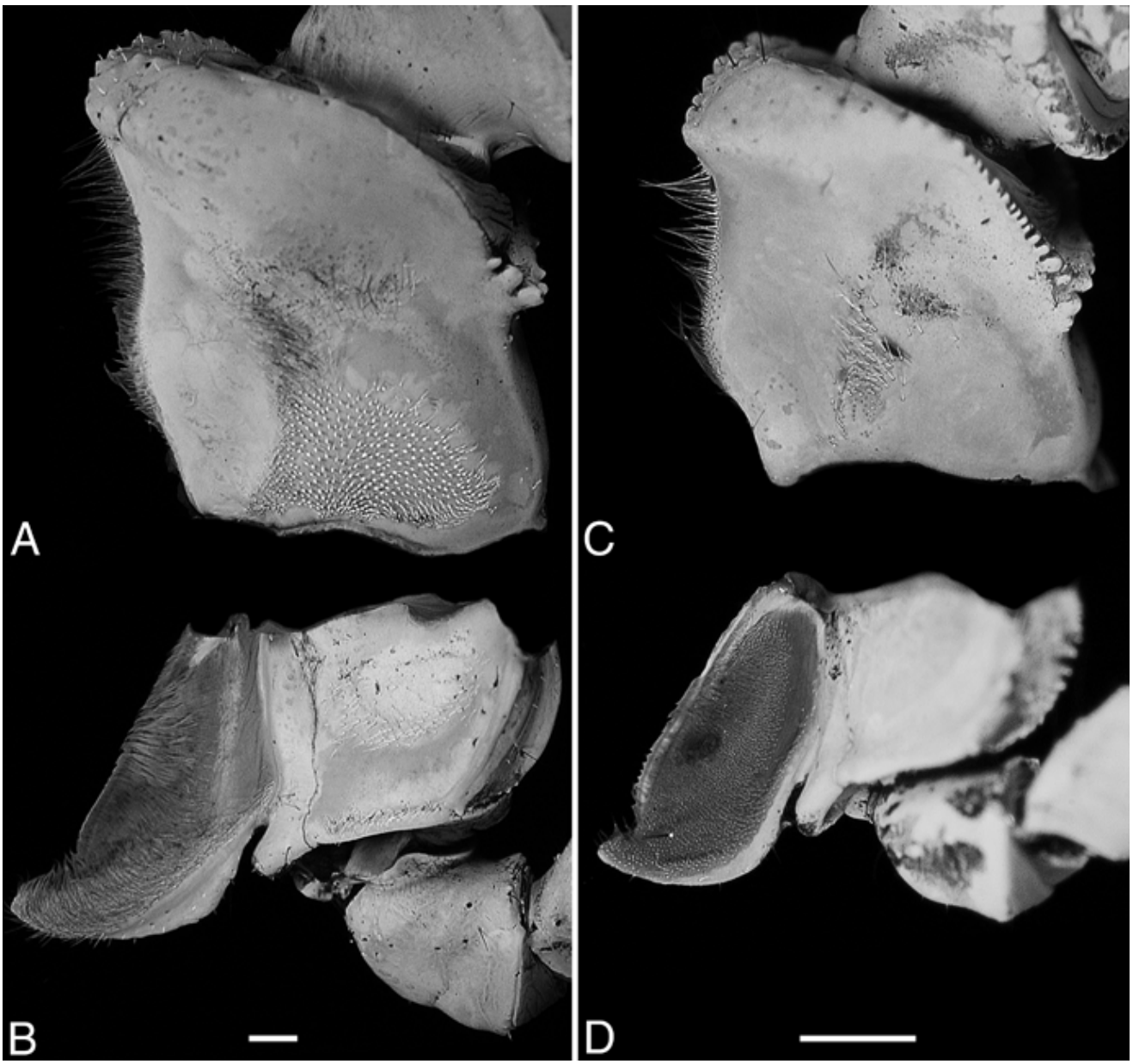

Fig. 17. Sinistral coxae of pedipalp, ventral aspect (*A*, *C*), and first leg, dorsal aspect (*B*, *D*), of representative scorpionids, illustrating macrosetae and surface macrosculpture. *A*, *B*, *Heterometrus spinifer* (Ehrenberg, 1828), ♀ (AMNH). *C*, *D*, *Opistophthalmus capensis* (Herbst, 1800), ♂ (AMNH). Scale bars = 1 mm.

verify given the fact that the distributions of most species traded (including *Opistophthalmus*) extend beyond South African borders, and dealers usually cite neighbouring states with relaxed collecting and export regulations (e.g. Mozambique) as sources. However, a recent article in a Czech aquarium magazine by Kovařík (2000*a*), on captive husbandry of the endemic South African *O. latimanus* C. L. Koch, 1841, provides conclusive evidence that scorpions have been collected and exported (probably illegally) from South Africa. As with *Heterometrus*, *Scorpio* and most species of *Pandinus*, species of *Opistophthalmus* are not listed by CITES and there is little or no regulation on their harvesting from the wild, a situation that is clearly inadequate for safe-guarding their future survival.

Genus ***Pandinus*** Thorell

Pandinus Thorell, 1876*a*: 12. Type species, by original designation: *Pandinus imperator* (C. L. Koch, 1841), as a pre–1758 name '*Pandinus africanus* (Linnaeus, 1758)'.

Pandinus: Thorell, 1876*b*: 84; Karsch, 1879*a*: 20; Kraepelin, 1899: 116; Birula, 1917*a*: 161; 1917*b*: 59; 1927: 86–88; Werner, 1934: 278; Kästner, 1941: 234; Bücherl, 1964: 59; Vachon, 1974: 953;

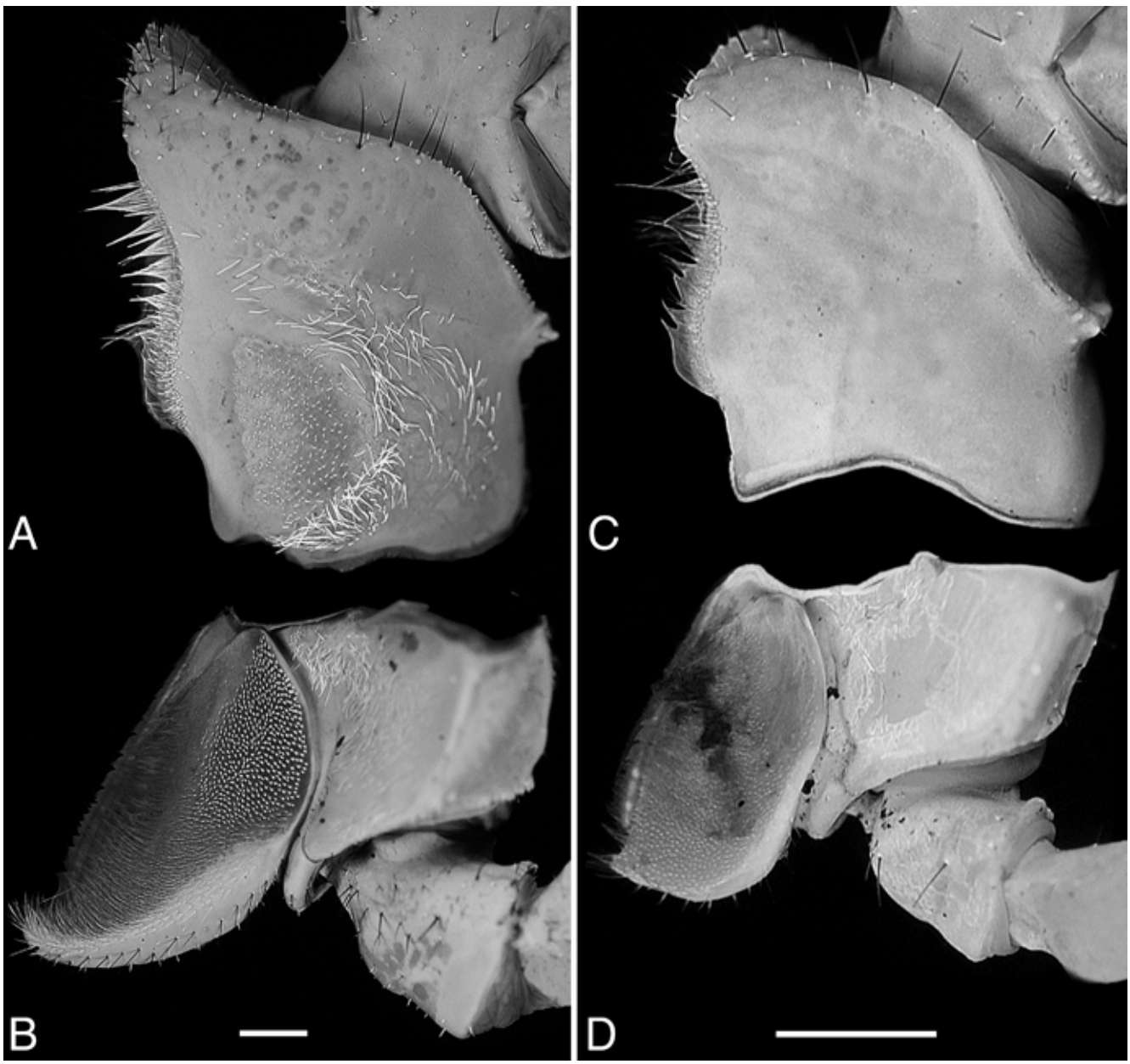

Fig. 18. Sinistral coxae of pedipalp, ventral aspect (*A*, *C*), and first leg, dorsal aspect (*B*, *D*), of representative scorpionids, illustrating macrosetae and surface macrosculpture. *A*, *B*, *Pandinus imperator* (C. L. Koch, 1841), ♂ (AMNH). *C*, *D*, *Scorpio maurus palmatus* (Ehrenberg, 1828), ♀ (AMNH). Scale bars = 1 mm.

Lourenço, 1989: 174; Sissom, 1990: 136; Nenilin & Fet, 1992: 15–17, 19; Kovařík, 1998: 140; Fet, 2000: 465; Lourenço, 2000: 25; Prendini, 2000*a*: 44.

Scorpio: Pocock, 1888: 245 (part); Pocock, 1893: 305 (part); Lönnberg, 1897: 197 (part); Kraepelin, 1894: 28 (part); Pocock, 1896*c*: 77.

Pandinus includes some of the largest extant scorpions, for example *P. dictator* and *P. imperator*, which can reach 170–200 mm in length (Vachon 1952*b*; Newlands 1987; Sissom 1990). Although no comprehensive revision currently exists for the genus, partial keys can be found in Pocock (1888, 1900*c*), Belfield (1956), Probst (1973), Vachon (1974), Lourenço and Cloudsley-Thompson (1996) and Kovařík (2000*a*).

Vachon (1967) elevated *P. gambiensis* Pocock, 1899, previously regarded as a subspecies of *P. imperator*, to the rank of species. Vachon (1974) redefined the two subgenera recognised at the time, and created three new ones, but neglected to allocate one species, *P. boschisi* Caporiacco, 1937, to subgenus. As two of Vachon's (1974) subgenera (*Pandinoides* and *Pandinurus*) were published without designating type species, they were not available in terms of the ICZN (1985), hence Fet (1997) designated type species for both subgenera, which now bear his name as author. One of the other subgenera, *Pandinops* Birula, 1913, was recently redefined by Kovařík (2000*b*), who also synonymised *P. pugilator* Pocock, 1900 with *P. bellicosus* (L. Koch, 1875) and described a new species, *P. pococki* Kovařík, 2000.

Regardless of these emendations, the cladistic validity of the subgenera of *Pandinus*, which are defined solely on the basis of differences in the counts of pedipalp trichobothria, remains to be tested. Their dubious validity is evidenced by the obviously erroneous placement of species that, despite differing slightly in trichobothrial count, appear to be closely related on the basis of other morphological characters, as well as DNA sequence data. Examples include the West African species *P. dictator* and *P. imperator*, respectively placed in *Pandinopsis* Vachon, 1974 and the nominal subgenus, and the east African species *P. cavimanus* and *P. viatoris* (Pocock, 1890), respectively placed in *Pandinoides* Fet, 1997 and *Pandinurus* Fet, 1997. Apparently, F. Kovařík and B. Striffler are currently revising the genus independently (personal communications). Their studies would be advised to address such issues.

Diagnosis

Pandinus is the sister-genus of *Heterometrus* (Prendini 2000*a*). The genera share the following characters, by which they can be separated from *Opistophthalmus* and *Scorpio*: presence of a stridulatory organ, comprising a 'rasp' (granular tubercles) and 'scraper' (stridulatory setae or scaphotrix), on opposing surfaces of the coxae of the pedipalps and the first pair of legs; equal counts of ventrosubmedian spiniform macrosetae on telotarsi I–II and III–IV. *Pandinus* can be separated from *Heterometrus* by the following characters: pedipalps neobothriotaxic major, with more than 26 trichobothria (patella with more than 13 trichobothria in *e* series and more than 3 trichobothria in *v* series; chela usually with more than 4 trichobothria in *V* series and occasionally with more than 2 trichobothria in *i* series); granular tubercles of 'rasp' and stridulatory setae (scaphotrix) of 'scraper' situated on coxae of pedipalp and first leg, respectively. *Pandinus* can be further separated from *Opistophthalmus* by the following characters: cheliceral coxae without stridulatory setae (scaphotrix) on dorsointernal surfaces, and chemoreceptive lamelliform setae (trichocopae) on internomedian surfaces. *Pandinus* can be further separated from *Scorpio* by the following characters: digital carina of pedipalp chela obsolete; pedipalps neobothriotaxic major, with more than 26 trichobothria.

Description

The following account provides the first description of this genus since Kraepelin (1899). Characters that are invariant within the Scorpionidae are omitted.

Colour. Usually entirely dark brown or black with pale telson (seldom with pale legs).

Carapace. Median notch in anterior margin present, deep (Fig. 9*C*); rostrolateral margin with or without a distinct notch next to posterior lateral ocelli. Median longitudinal sulcus narrow, suturiform, with or without a distinct anterior furcation; anteromedian and anterocular depressions absent. Posterior carapacial sutures present but may be indistinct. Three pairs of lateral ocelli. Median ocular tubercle raised, situated medially; superciliary carinae higher than ocelli, not extended anteriorly or posteriorly. Surfaces of carapace finely to coarsely granular laterally, smooth to coarsely granular in interocular region, and smooth posteromedially (♂, ♀).

Chelicerae. Movable finger with distal external and distal internal teeth not opposable to moderately opposable (Fig. 10*E*, *F*). Cheliceral coxae without stridulatory setae (scaphotrix) on dorsointernal surfaces and chemoreceptive lamelliform setae (trichocopae) on internomedian surfaces.

Pedipalps. Chela surface reticulate to coarsely granular. Chela dorsal secondary, subdigital, digital and ventromedian carinae obsolete (Fig. 13). Chela fingers granular; second lobe of movable finger (♂) usually more strongly developed than other lobes, with correspondingly well-developed notch in fixed finger; externodistal edge of fixed finger with deep notch for terminal denticle of movable finger.

Patella with anterior process obsolete and dorsal surface convex, dorsomedian carina raised above horizontal axis of dorsoexternal carina; dorsomedian, ventroexternal and paired externomedian carinae obsolete to absent (Fig. 16*A–C*); dorsoexternal and internomedian carinae obsolete, moderately or well developed. Internomedian carina seldom comprising enlarged spiniform granules.

Femur dorsoexternal carina present and more strongly developed than dorsointernal carina, which is obsolete or absent; internomedian carina oriented diagonally between ventrointernal and dorsointernal carinae; ventroexternal and ventroexternal secondary carinae absent.

Trichobothria. Pedipalps type C neobothriotaxic major (Figs 13, 16*A–C*), with more than 26 trichobothria (patella with more than 13 trichobothria in *e* series and more than 3 trichobothria in *v* series; chela usually with more than 4 trichobothria in *V* series and occasionally with more than 2 trichobothria in *i* series). Femur with trichobothrium *i* located on dorsal surface.

Pectines. Internal fulcral plates smooth proximally but densely setose (microsetae only) distally. First proximal median lamella of each pecten usually with mesial margin angular and pectinal teeth present along entire posterior margin (with mesial margin shallowly curved and proximal region of posterior margin devoid of teeth in some). Pectinal teeth (♂) straight and elongate.

Genital operculum. Genital opercula (♂) usually overlapping partially.

Legs. First pair of maxillary lobes (coxapophyses) rounded–truncate anteriorly and roughly equal in length to second pair or tapering anteriorly, longer than, and encircling second pair. Stridulatory organs, comprising a 'rasp' (granular tubercles) and 'scraper' (stridulatory setae or scaphotrix), present on opposing surfaces of coxae of pedipalp (Fig. 18*A*) and first leg (Fig. 18*B*), respectively. Femora each with paired carinae on prolateral surface. Tibiae I and II and basitarsi I and II each with a retrolateral row of spiniform macrosetae. Telotarsi I–IV short, stout and distally broadened in dorsal and lateral views, with dorsomedian lobe approximately equal to laterodistal lobes; telotarsi each with paired ventrosubmedian rows of spiniform macrosetae, 2–4 of which are inserted on laterodistal lobes; counts of ventrosubmedian spiniform macrosetae equal on telotarsi I–II and III–IV (Fig. 20*A–D*).

Mesosoma. Post-tergites smooth medially and coarsely granular laterally, to entirely coarsely granular. Sternites usually smooth (♂, ♀; Fig. 21*C*), but VII granular or tuberculate (♂) in some, such as *P. colei*. Sternite VII usually acarinate or with a pair of obsolete ventrolateral carinae, but with four strongly developed carinae (paired ventrosubmedian and ventrolateral) in some, such as *P. cavimanus*.

Metasoma and telson. Metasomal segments I–IV each with paired ventrosubmedian and ventrolateral carinae, usually equally developed on all segments (Fig. 21*C*), rarely obsolete, but more strongly developed on segments I and II in some, such as *P. cavimanus*; intercarinal surfaces sparsely granular, except for ventral surfaces of segments I–III, which are usually smooth (♂, ♀), but tuberculate (♂) in some, such as *P. colei*. Segment V smooth or granular dorsally, granular ventrally; ventrolateral carinae comprising spiniform denticles or rounded granules; distal portion of ventromedian carina continuous. Telson vesicle granular ventrally, smooth laterally.

Male reproductive anatomy. Hemispermatophore with distal lamina truncate distally, without an accessory distal lobe protruding between articular suture and distal lobe (hook).

Included taxa

Pandinus currently includes 24 species and two subspecies, placed into five subgenera (Vachon 1967, 1974; Lamoral and Reynders 1975; Fet 2000; Kovařík 2000*b*): *Pandinoides* Fet, 1997; *Pandinops* Birula, 1913; *Pandinopsis* Vachon, 1974; *Pandinurus* Fet, 1997; and *Pandinus* Thorell, 1876. One species has not been allocated to subgenus.

Ecology

Ecological data are largely unavailable for the remaining species of *Pandinus*. However, the thickened metasoma, short, robust legs with stout, spiniform macrosetae distributed laterally and distally on the basitarsi, and curved telotarsal ungues of all species in the genus are indicative of a fossorial, and essentially pelophilous, habit, as is the case in *P. imperator*. The limited data available for other species—*P. cavimanus*, *P. dictator*, *P. gregoryi* (Pocock, 1896) and *P. viatoris*—confirm their ability to burrow and, in the case of *P. dictator* and *P. viatoris*, to cohabit with minimal aggression or cannibalism (Newlands 1987; personal observation). Unlike *Opistophthalmus*, no described species of *Pandinus* exhibits psammophilous or lithophilous adaptations.The ecology, behaviour and ecophysiology of *P. imperator* have been extensively studied (e.g. Toye 1970; Garnier and Stockmann 1972; Casper 1985; Mahsberg 1990). Burrows are preferentially constructed in termite mounds and under stones or logs, and may contain up to 20 individuals, with the largest nearest the entrance (Toye 1970; Polis and Lourenço 1986; Mahsberg 1990). Mixed age groups of related and unrelated individuals cohabit with minimal aggression or cannibalism in laboratory terraria, and group living has been demonstrated to contribute significantly to postembryonic growth rate and survival probability, especially among kin (Mahsberg 1990; Kriesch 1994). *Pandinus imperator* is known for its unusual activity rhythms. Diurnal activity has frequently been observed in this species, which may appear on the surface in large numbers, especially after rain (Toye 1970; Newlands 1987).

Distribution

Africa: Benin, Burkina Faso, Cameroon, Central African Republic, Chad, Congo, Côte d'Ivoire, Democratic Republic of Congo, Equatorial Guinea (including Bioko Island), Eritrea, Ethiopia, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Kenya, Liberia, Malawi, Mali, Mozambique, Nigeria, Senegal, Sierra Leone, Somalia, Sudan, Tanzania, Togo, Zambia. Asia: Saudi Arabia, Yemen.

Fig. 19. Dextral tarsi I–IV of representative scorpionids, illustrating ungues and macrosetae in ventrolateral aspect. *A–D*, *Heterometrus spinifer* (Ehrenberg, 1828), ♀ (AMNH). *E–H*, *Opistophthalmus capensis* (Herbst, 1800), ♂ (AMNH). Scale bars = 1 mm.

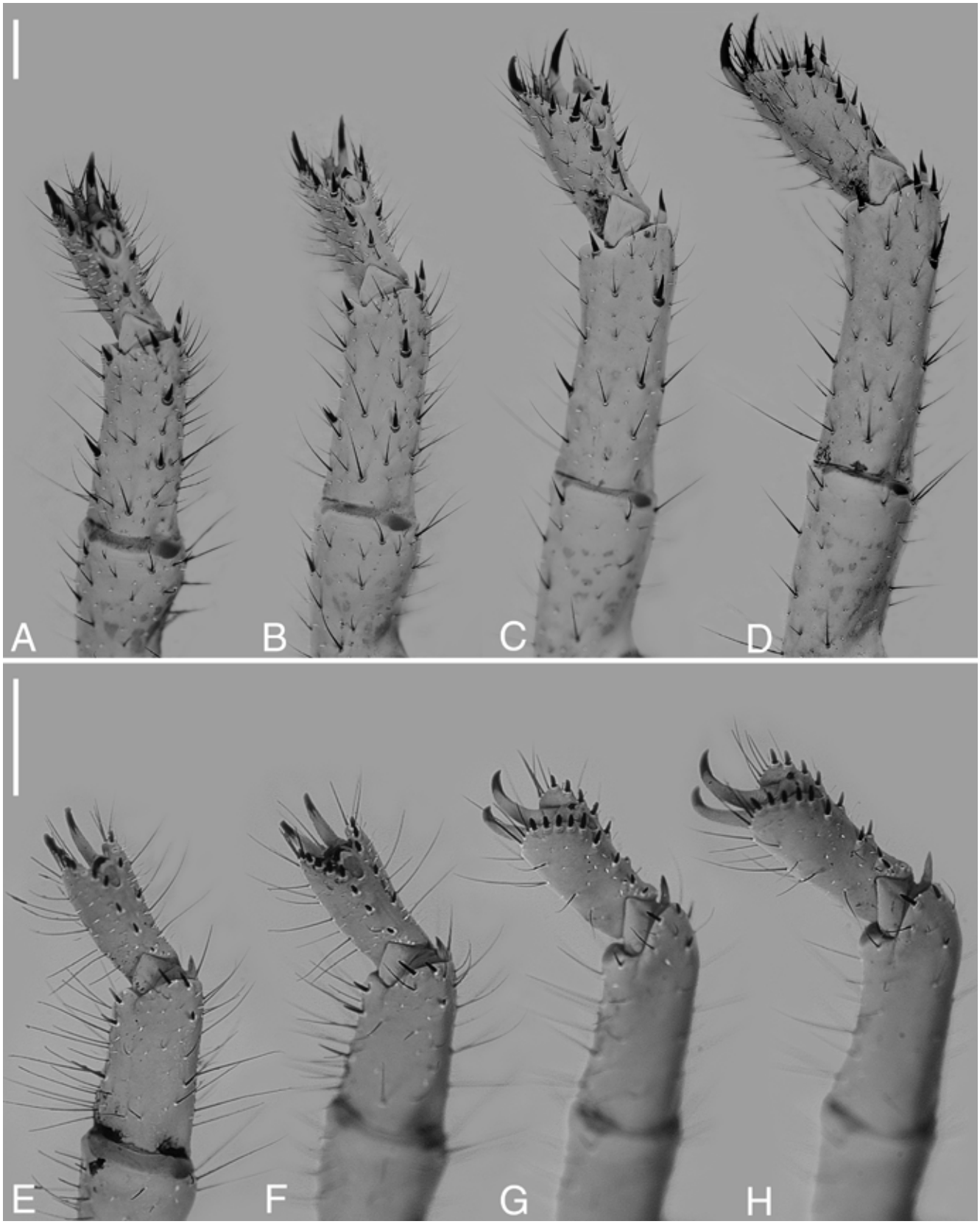

Fig. 20. Dextral tarsi I–IV of representative scorpionids, illustrating ungues and macrosetae in ventrolateral aspect. *A–D*, *Pandinus imperator* (C. L. Koch, 1841), ♂ (AMNH). *E–H*, *Scorpio maurus palmatus* (Ehrenberg, 1828), ♀ (AMNH). Scale bars = 1 mm.

Pandinus is distributed from the tropical rainforest and mesic savanna of western and central Africa to the arid savanna and semi-desert of eastern Africa and the southern Arabian Peninsula. Species of *Pandinus* have not been recorded from Burundi, Djibouti, Rwanda or Uganda, but are suspected to occur in some or all of those countries. At least one specimen of a *Pandinus* species has been recorded from Chad (MRAC 111.190), and another from Central African Republic (AHC 1844). Several authors (Lamoral and Reynders 1975; Fet 2000) listed *P. viatoris* as occurring in Zimbabwe, apparently based on Hirst's (1911) records from Petauke and Broken Hill [Kabwe]. Hewitt (1918: 152) also mentioned these records but noted that *P. viatoris* 'is not known to the Rhodesian Museum from South Rhodesia [Zimbabwe]'. These localities actually occur in Zambia (formerly North Rhodesia) and it appears that *Pandinus* does not occur south of the Zambezi River. The distributions of the three West African species were mapped by Vachon (1970) and Prendini (in press).

Conservation status

Several species of *Pandinus* (e.g. *P. cavimanus*, *P. imperator* and *P. viatoris*) are readily available in Europe, the USA and Japan for the international trade in exotic pets. Most of these appear to originate from Ghana and Côte d'Ivoire (*P. imperator*, the 'emperor scorpion') and Tanzania (*P. cavimanus*, the 'red-claw scorpion', and *P. viatoris*). Several specimens of *P. colei* were recently imported to the USA from Ethiopia (R. D. Gaban, personal observation). Dupré (1992) records *P. cavimanus* as being imported to France from Kenya and additionally records *P. dictator* as being imported from Cameroon. *Pandinus imperator* is probably the most common species of scorpion in the exotic pet trade, for which an extensive literature on captive husbandry and breeding exists (e.g. Larrouy *et al.* 1973; Garnier 1974; Hull-Williams 1986; Krapf 1988; Copeland 1990; Dupré 1990; Montambaux 1996; Schiejok 1997; Mahsberg *et al.* 1999; Rubio 2000).

As with *Heterometrus*, the remaining wild populations of *P. imperator* are vulnerable to overharvesting for the pet trade owing to their long gestation period (at least 7 months), small brood sizes (30–35), age to sexual maturity (4–7 years) and parental care (Vachon *et al.* 1970; Larrouy *et al.* 1973; Polis and Lourenço 1986; Mahsberg 1990; Polis and Sissom 1990). Furthermore, wild populations are threatened not only by overexploitation but by continuing destruction of their habitat through deforestation. The decline in *P. imperator* may be partially alleviated by its recent CITES status (IUCN 1994; Lourenço and Cloudsley-Thompson 1996) and the ease with which it may be bred in captivity. However, it is unclear whether the CITES status has had any impact in protecting the remaining wild populations, because wild-caught specimens continue to be advertised alongside captive-bred specimens by all major dealers. Moreover, although two other closely related species, *P. dictator* and *P. gambiensis*, were also provided CITES status, these are rarely, if ever, available in the pet trade whereas others that are available (especially *P. cavimanus*) have no CITES status. The conservation status of the remaining species of *Pandinus* is presently unknown, but the restricted ranges of most are cause for concern.

Genus ***Scorpio*** Linnaeus

Scorpio Linnaeus, 1758: 624, 625 (part); 1767: 1037, 1038 (part); Latreille, 1810: 116 (part); 1817: 103 (part); Sundevall, 1833: 30, 31 (part); Karsch, 1879*a*: 16 (part); Pocock, 1888: 246 (part); Kraepelin, 1899: 123, 124; Birula, 1910: 115; Kraepelin, 1913: 185; Birula, 1917*a*: 161; 1917*b*: 59; Werner, 1934: 278; Kästner, 1941: 234; Vachon, 1950: 156–161; 1952*a*: 328–333; Bücherl, 1964: 59; Levy & Amitai, 1980: 102, 103; Francke, 1985: 12, 18; Lourenço, 1989: 174; Sissom, 1990: 136; Nenilin & Fet, 1992: 17, 18; Kovařík, 1998: 141; Fet, 2000: 473; Lourenço, 2000: 25, 37; Prendini, 2000*a*: 44. Type species, by subsequent designation (Karsch, 1879*a*: 19): *Scorpio maurus* Linnaeus, 1758[8].

Scorpion: Latreille, 1817: 106; 1825: 310.

Buthus (*Heterometrus*): Ehrenberg in Hemprich & Ehrenberg, 1828 (part): pl. I, fig. 1.

Heterometrus (*nec* Ehrenberg 1828): Peters, 1861: 512; Simon, 1872: 258; Thorell, 1876*b*: 84; Simon, 1879: 92; Kraepelin, 1894: 73; Lönnberg, 1897: 197.

As currently recognised, this genus comprises a single widespread, polymorphic species, *S. maurus*, with 19 official subspecies (Fet 2000), for which detailed revisions and keys were published by Birula (1910), and, for the North African subspecies, by Vachon (1950, 1952*a*). Birula (1910) arranged the subspecies of *S. maurus* into two groups, the 'sectio *maurus*' (with seven subspecies) and 'sectio *propinquus*' (with four Asian subspecies), but their status was never reconsidered (Fet 2000). Further discussion of the diagnostic differences among subspecies inhabiting particular geographical regions can be found in Vachon (1979) for Saudi Arabia, Levy and Amitai (1980) for Israel, and Sissom (1994) for Yemen.

The taxonomy of this genus is outdated and, by all accounts, contradictory. Pocock (1900*c*) originally stated that all the forms described are valid species. However, later authors (e.g. Vachon 1950, 1952*a*; Levy and Amitai 1980) maintained that the characters used for their distinction (coloration, granulation, counts of pectinal teeth and spiniform macrosetae of the telotarsi, shape of the pectinal proximal median lamella) exhibit considerable variation when many specimens of a population are examined. According to these authors, there are no reliable characters for distinction of the subspecies and the absence of such characters precludes their recognition as species. Nevertheless, they have provided keys by which the subspecies may be consistently diagnosed.

Clearly, most, if not all, the subspecies of *S. maurus* should be regarded as phylogenetic species for the following reasons. First, previous authors were indeed able to differentiate subspecies on morphological criteria, as evidenced by the diagnoses and identification keys that they provided. Second, no evidence has been presented to suggest that the morphological variation in *S. maurus* is clinal or that the various subspecies are panmictic, basic predictions of the hypothesis that this is a widespread polymorphic species (Dobzhansky 1937; Mayr 1963; Paterson 1985). Indeed, some of the subspecies appear to be geographically isolated, for example *S. maurus occidentalis* Werner, 1936. Others that are parapatric occur in sympatry at the periphery of their distributions (Levy and Amitai 1980), for example *S. maurus fuscus* and *S. maurus palmatus*, and must therefore be reproductively isolated. Finally, at least some of the subspecies differ markedly in their ecological requirements, and may therefore be regarded as ecological species (Van Valen 1976). For example, Levy and Amitai (1980) provided conclusive evidence that *S. maurus fuscus* and *S. maurus palmatus* differ in their substratum preferences and in the structure of their burrows, as has been demonstrated in other fossorial scorpionids (Newlands 1972*a*, 1972*b*, 1978; Eastwood 1978*a*, 1978*b*; Lamoral 1978*a*, 1979), and urodacids (Koch 1977). If ecological attributes are regarded as phylogenetic characters (e.g. Wenzel 1993), these subspecies must also be regarded as phylogenetic species.

The distributions of the subspecies of *S. maurus* conform to the typical pattern of localised endemics exhibited among species of the other African scorpionid genera, *Pandinus* and *Opistophthalmus*, suggesting that similar mechanisms of speciation have operated in all. The only difference between *Scorpio* and these genera is that the taxa within *Scorpio* have not diverged to the same extent, which may be nothing more than a reflection of the relatively recent onset of aridification in northern Africa in the late Miocene to early Pliocene (<8 million years ago; Axelrod and Raven 1978; van Zinderen Bakker 1978, 1980; Pickford and Senut 2000). Less time for morphological divergence may explain why the taxa recognised within *Scorpio* are more similar morphologically than those recognised within *Pandinus* or *Opistophthalmus*. A thorough taxonomic revision of *Scorpio*, applying modern concepts and techniques (including a cladistic analysis, based on morphological and molecular data) is overdue.

Diagnosis

Scorpio is the sister-genus of the monophyletic group comprising (*Heterometrus* + *Pandinus*). *Scorpio* can be separated from *Heterometrus* and *Pandinus* by the following characters: absence of a stridulatory organ, comprising a 'rasp' (granular tubercles) and 'scraper' (stridulatory setae or scaphotrix), on opposing surfaces of the coxae of the pedipalps and the first pair of legs; digital carina of pedipalp chela usually distinct; counts of ventrosubmedian spiniform macrosetae increasing from telotarsi I–II to III–IV. *Scorpio* can be further separated from *Heterometrus* by the following character: sternite VII with paired ventrosubmedian and ventrolateral carinae. *Scorpio* can be further separated from *Pandinus* by the following character: pedipalps orthobothriotaxic, with 26 trichobothria (patella with 13 trichobothria in *e* series and 3 trichobothria in *v* series; chela with 4 trichobothria in *V* series and 2 trichobothria in *i* series). *Scorpio* can be separated from *Opistophthalmus* by the following characters: pedipalps orthobothriotaxic, with 26 trichobothria (including 13 trichobothria in *e* series of patella); cheliceral coxae without stridulatory setae (scaphotrix) on dorsointernal surfaces, and chemoreceptive lamelliform setae (trichocopae) on internomedian surfaces.

Description

The following account updates and enlarges on the generic descriptions provided by Vachon (1952*a*) and Levy and Amitai (1980). Characters that are invariant within the Scorpionidae are omitted.

Colour. Varies from dark brown with pale legs to entirely pale. Telson usually not markedly paler than metasoma.

Carapace. Median notch present in anterior margin, but shallow (Fig. 9*D*); rostrolateral margin entire. Median longitudinal sulcus narrow, suturiform, with weak anterior furcation; anteromedian and anterocular depressions absent. Posterior carapacial sutures present. Three pairs of lateral ocelli. Median ocular tubercle shallow, situated medially; superciliary carinae usually lower than ocelli, not extended anteriorly or posteriorly. Surfaces of carapace finely to coarsely granular laterally, smooth (♀) to coarsely granular (♂) in interocular region, and smooth (♀) to coarsely granular (♂) posteromedially.

Chelicerae. Movable finger with distal external and distal internal teeth not opposable (Fig. 10*G*, *H*). Cheliceral coxae without stridulatory setae (scaphotrix) on dorsointernal surfaces and chemoreceptive lamelliform setae (trichocopae) on internomedian surfaces.

Pedipalps. Chela surface coarsely granular. Chela ventromedian carina distinct; dorsal secondary, subdigital and digital carinae usually distinct (Fig. 14). Chela fingers smooth; second lobe of movable finger (♂) not larger than other lobes; externodistal edge of fixed finger with shallow notch for terminal denticle of movable finger.

Patella with anterior process obsolete and dorsal surface convex, dorsomedian carina raised above horizontal axis of dorsoexternal carina (Fig. 16*D*, *E*); dorsoexternal, dorsomedian and internomedian carinae obsolete; ventroexternal and paired externomedian carinae distinct (Fig. 16*E*, *F*).

Femur dorsoexternal carina usually less strongly developed than dorsointernal carina; internomedian carina oriented diagonally between ventrointernal and

dorsointernal carinae; ventroexternal and ventroexternal secondary carinae absent.

Trichobothria. Pedipalps type C orthobothriotaxic (Figs 14, 16*D–F*), with 26 trichobothria (patella with 13 trichobothria in *e* series and 3 trichobothria in *v* series; chela with 4 trichobothria in *V* series and 2 trichobothria in *i* series). Femur with trichobothrium *i* located on internal surface.

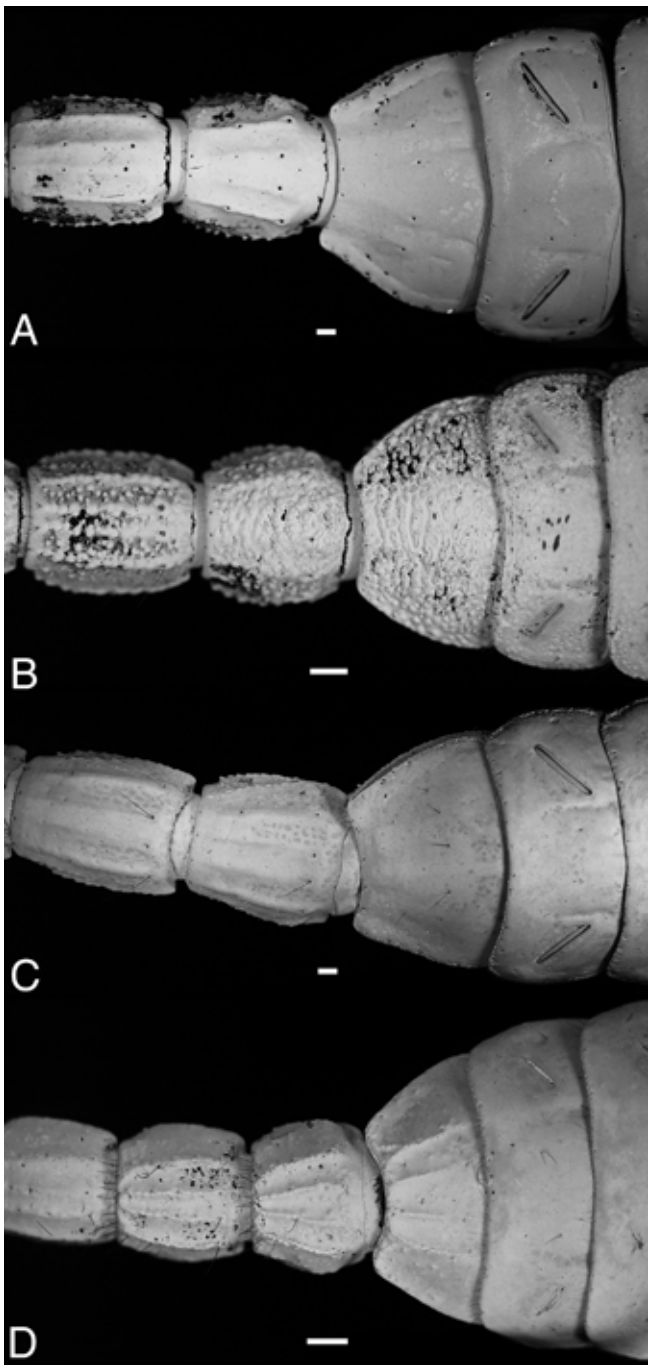

Fig. 21. Sternite VII and ventral surface of metasomal segments I and II of representative scorpionids, illustrating surface macrosculpture. *A*, *Heterometrus spinifer* (Ehrenberg, 1828), ♀ (AMNH). *B*, *Opistophthalmus capensis* (Herbst, 1800), ♂ (AMNH). *C*, *Pandinus imperator* (C. L. Koch, 1841), ♂ (AMNH). *D*, *Scorpio maurus palmatus* (Ehrenberg, 1828), ♀ (AMNH). Scale bars = 1 mm.

Pectines. Internal fulcral plates sparsely setose (macrosetae scattered over entire surface). First proximal median lamella of each pecten with mesial margin angular and pectinal teeth present along entire posterior margin. Pectinal teeth (♂) short and curved.

Genital operculum. Genital opercula (♂) not overlapping.

Legs. First pair of maxillary lobes (coxapophyses) rounded–truncate anteriorly and roughly equal in length to second pair. Stridulatory organs, comprising a 'rasp' (granular tubercles) and 'scraper' (stridulatory setae or scaphotrix), absent from opposing surfaces of coxae of pedipalps and first pair of legs (Fig. 18*C*, *D*). Tibiae I and II and basitarsi I and II each with a retrolateral row of spiniform macrosetae (Fig. 20*E*, *F*). Femora each with a single carina on prolateral surface. Telotarsi I–IV short, stout and distally broadened in dorsal and lateral views, with dorsomedian lobe approximately equal to laterodistal lobes; telotarsi each with paired ventrosubmedian rows of spiniform macrosetae, 3–5 of which are inserted on laterodistal lobes (Fig. 20*E–H*); counts of ventrosubmedian spiniform macrosetae increasing from telotarsi I–II to III–IV.

Mesosoma. Post-tergites smooth (♀) or coarsely granular (♂). Sternites III–VI smooth (♀), III–VI rugose and VII granular (♂). Sternite VII with four strongly developed carinae (paired ventrosubmedian and ventrolateral, Fig. 21*D*).

Metasoma and telson. Metasomal segments I–IV each with paired ventrosubmedian and ventrolateral carinae, which are more strongly developed on segments I–II (Fig. 21*D*); intercarinal surfaces granular (♂, ♀). Segment V granular dorsally and ventrally; ventrolateral carinae comprising rounded granules; distal portion of ventromedian carina breaking up into numerous granules. Telson vesicle granular ventrally and usually also laterally.

Male reproductive anatomy. Hemispermatophore with distal lamina truncate distally, without an accessory distal lobe protruding between articular suture and distal lobe (hook).

Included taxa

One species with 19 subspecies.

Ecology

All subspecies of *Scorpio* appear to be obligate burrowers, constructing burrows under stones or in open ground by means of their chelicerae, short, robust legs with stout, spiniform macrosetae distributed laterally and distally on the basitarsi, curved telotarsal ungues and thickened metasoma. In contrast with *Opistophthalmus*, no subspecies of *Scorpio* exhibits psammophilous or lithophilous adaptations, although

different subspecies exhibit specific substratum preferences. High densities of burrows occur in suitable habitat but, unlike *Heterometrus* and *Pandinus*, cohabitation of multiple individuals within a single burrow (except during courtship or parental care) and the communal construction of burrows are absent (Levy and Amitai 1980; Shachak and Brand 1983).

Although ecological data are unavailable for most subspecies, *S. maurus fuscus* and *S. maurus palmatus*, occurring allopatrically in Israel, have been extensively studied (Levy and Amitai 1980; Shachak and Brand 1983; Kotzman *et al.* 1989; Danin 1994; Rutin 1996), while ecological studies on *S. maurus fuscus* have also been conducted in neighbouring Jordan and Turkey (Amr and El-Oran 1994; Crucitti 1999). These subspecies differ markedly in their substratum requirements, *S. maurus fuscus* preferring harder soils such as terra rossa, basalt and rendzina than *S. maurus palmatus*, which inhabits brown-red sandy soils, loess and alluvium (Levy and Amitai 1980). The subspecies also differ in their burrow structure. The burrows of *S. maurus palmatus* are always constructed in open ground and run parallel to the ground surface for approximately 10 cm, before turning downwards for 20–70 cm and ending in an enlarged chamber. The burrows of *S. maurus fuscus* are constructed in open ground or under stones and usually run vertically, without turns, to a depth of approximately 40 cm, where they end in an enlarged chamber. Mesosomal percussion, involving rapid drumming of the posterior sternites against the ground, has been observed in males of both subspecies (Rosin and Shulov 1961).

Distribution

Africa: Algeria, Egypt (including Sinai), Libya, Mauritania, Morocco, Senegal, Tunisia. Asia: Iraq, Iran, Israel, Jordan, Kuwait, Lebanon, Qatar, Saudi Arabia, Syria, Turkey, Yemen.

The broad distribution of *Scorpio* extends from Senegal and Morocco on the West African coast, along the Mediterranean to the Red Sea, and on through the Arabian Peninsula and the Middle East as far north as southern Turkey and as far east as central Iran. Although the full extent of the distribution has yet to be accurately mapped, it appears to be discontinuous, as evidenced by the occurrence of isolated populations on the West African coast (*S. maurus occidentalis*) and in the Hoggar and Tassili-n-Ajjer mountain ranges of southern Algeria (undescribed subspecies; Vachon 1952*a*; Kanter 1971). This disjunction is interpreted as relictual and attributed to range contraction associated with the onset of aridification in northern Africa (Niethammer 1971; Dumont 1982).

Scorpio has not been recorded from the Gambia, Oman, the United Arab Emirates or Western Sahara, but may occur in some or all of those countries. The genus does not extend to Ethiopia or to India as suggested by some authors (Birula 1925; Levy and Amitai 1980). Vachon (1950) rejected Pallary's (1938) record of *Scorpio* from the central Congo, but Levy and Amitai (1980) suggested that the genus could occur there. As with records from Tanzania (as 'Tanganyika') cited in recent catalogues (e.g. Lamoral and Reynders 1975; Fet 2000), this record is probably attributable to a misidentification of *Pandinus*.

Conservation status

Perhaps because of its smaller size and more specialised ecological requirements (necessitating more elaborate methods for successful captive husbandry), *Scorpio* appears to be less popular in the exotic pet trade and thus more seldom offered. Nonetheless, at least one subspecies, *S. maurus palmatus* (apparently imported from Egypt), is available almost year-round in Europe, the USA and Japan (Hull-Williams 1986; Mahsberg *et al.* 1999; Rubio 2000). Another subspecies, *S. maurus fuscus* (imported from Israel) is rarely available. Life-history parameters similar to those of *Heterometrus*, *Opistophthalmus* and *Pandinus*, including long gestation period (14–15 months), small brood sizes (8–25), age to sexual maturity (3–4 years) and parental care (Birula 1917*b*; Levy and Amitai 1980; Shachak and Brand 1983; Polis and Lourenço 1986; Crucitti 1999), together with restricted distributions, render *Scorpio* vulnerable to overharvesting. Fortunately, the reduced demand for *Scorpio* in the pet trade, together with their occurrence in many countries from which exportation of wildlife is strictly prohibited and in arid to semi-arid habitats that are less vulnerable to destruction than the rainforests inhabited by many species of *Heterometrus* and *Pandinus*, suggests that their survival is assured.

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Endnotes

1. The ICZN Direction 60 (1957) placed Scorpionidae on the Official List of Family-Group Names in Zoology as an earliest family-group name (as Scorpionides) authored by Leach (1814). However, according to Fet (2000), Latreille (1802) is the correct author of this name.
2. Simon (1879) formed the new family name Heterometridae based on the generic name *Heterometrus* Ehrenberg, 1828. Although

Simon misidentified *Scorpio* Linnaeus, 1758 as *Heterometrus* Ehrenberg, his name is still valid (Fet 2000).

3. Constantinou and Cloudsley-Thompson's (1984) scanning electron micrographs revealed the presence in *Scorpio* of an area of granules on opposing surfaces of the coxae of the pedipalps and first pair of legs, which appears to be positionally homologous with the stridulatory surfaces of *Heterometrus* and *Pandinus* (Prendini 2000*a*). However, this 'stridulatory surface' appears to be vestigial (stridulation has never been recorded in *Scorpio*) and, since it is barely visible under a light microscope, may as well be regarded as absent for diagnostic purposes.
4. According to Fet (2000), the name *Centrurus* Ehrenberg, 1829 was a subject of confusion. Its type was not designated in the original description but by subsequent monotypy as *Centrurus galbineus* C. L. Koch, 1838 (without type locality). Later, Peters (1861: 511–512) stated that *Centrurus sensu* C. L. Koch, 1838 was a different genus from Ehrenberg's, and introduced a new replacement name, *Dacurus* Peters, 1861, with '*Centrurus galbineus* Koch from Central America' as its type. Karsch (1879*a*) demonstrated that *Dacurus galbineus sensu* Peters, 1861 belonged to the genus *Opisthacanthus* (Ischnuridae), and introduced a new replacement name, *Caucon* Karsch, 1879, for *Centrurus sensu* C. L. Koch, 1838. Later, Kraepelin (1894: 34) demonstrated that *Centrurus galbineus* C. L. Koch, 1838 was a synonym of the Asian *Heterometrus longimanus* (Herbst, 1800). Meanwhile, Thorell (1876*a*) incorrectly designated the type species of *Centrurus* Ehrenberg, 1829 as *Androctonus biaculeatus* Lucas, 1835 [= *Centruroides gracilis* (Latreille, 1804)] (Buthidae). Many authors since considered *Centrurus* to be the senior synonym of *Centruroides* Marx, 1890. However, it is actually a junior synonym of *Heterometrus* Ehrenberg, 1828, although this was obviously not Ehrenberg's intention (Fet 2000).
5. The generic name *Atreus* C. L. Koch, 1837 is a *lapsus calami* (Fet 2000). This name was created in a figure legend instead of *Opistophthalmus* C. L. Koch (Scorpionidae) and refers explicitly to *O. capensis* (Herbst, 1800). It is not available under Koch's authorship.
6. The original spelling of *Opistophthalmus* C. L. Koch, 1837 was changed to *Opisthophthalmus* by subsequent authors (except L. Koch and E. Simon) because C. L. Koch's (1837) name is an improper latinisation. Francke (1985) rejected this spelling as an unjustified emendation. Prendini (2001*e*) followed Fet (2000) in listing *Opistophthalmus* species without specifying the unjustified spelling by various authors.
7. The name *Oecopetrus* Pocock, 1893 was introduced as a substitute name for *Petrooicus* Karsch, 1879, believed to be a homonym of *Petroica* Swainson, 1829 (Aves, Passeriformes, Petroicidae). However, these names are not homonymous (Francke 1985; Fet 2000; Prendini 2001*e*).
8. Fet (2000) noted the following. Latreille (1810) designated *Scorpio europaeus* Linnaeus, 1758 as type species of the genus *Scorpio*. ICZN Opinion 104 (1928) placed this genus on the Official List of Generic Names in Zoology with *Scorpio europaeus* Linnaeus, 1758 as type species. The case was discussed in detail in the ICZN Direction 60 (1957), which considered application made by Hemming (1955) and validated Karsch's (1879*a*) decision on selection of *Scorpio maurus* Linnaeus, 1758 as the type species. The ICZN also suppressed 'the specific name *europaeus* Linnaeus, 1758, as published in the combination *Scorpio europaeus*', in amendment of a ruling given in the ICZN Opinion 104 (1928).

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Appendix 1. Terminal taxa, specimens and tissue samples used for cladistic analysis of the family Scorpionidae

Depositories for material examined are abbreviated as follows: AHC, Alexis Harington Private Collection, University of the Witwatersrand (Johannesburg, South Africa [now deposited in the AMNH]); AMNH, American Museum of Natural History (New York, NY); CAS, California Academy of Sciences (San Francisco, CA); FMNH, Field Museum of Natural History (Chicago, IL); MCZ, Museum of Comparative Zoology, Harvard University (Cambridge, MA); MRAC, Museé Royal de l'Afrique Centrale (Tervuren, Belgium); NMSA, Natal Museum (Pietermaritzburg, South Africa); NMNW, National Museum of Namibia (Windhoek, Namibia); SAMC, South African Museum (Cape Town, South Africa); USNM, US National Museum of Natural History, Smithsonian Institution (Washington, DC). Tissue samples are deposited in the Ambrose Monell Collection for Molecular and Microbial Research (AMCC) at the AMNH.

Outgroup

Nebo Simon, 1878. Nine species are recognised in this diplocentrid genus (Sissom and Fet 2000), which is the most basal of the Diplocentridae Karsch, 1880 (Stockwell 1989; Prendini 2000*a*). It is placed in a separate subfamily, Nebinae Kraepelin, 1905, from the remaining diplocentrid genera, placed in the Diplocentrinae Karsch, 1880, and the monophyly of both subfamilies is well supported (Stockwell 1989; Prendini 2000*a*). The type species of *Nebo* was included as an outgroup for the Scorpionidae.

1. *Nebo hierichonticus* (Simon, 1872). **Israel:** vi.1998, Y. Lubin, 1 juv. ♂ (AMCC 101694); Palestine, Afule, 25.ix.1934, Dr F. R. S. Shaw, 5 ♂ 2 ♀ (FMNH); Mt Carmel, 20.vii.1960, 1 subad. ♂ (CAS), 12.xi.1960, Dr M. R. Warburg, 1 juv. ♂ (CAS).

Ingroup

Heterometrus Ehrenberg, 1828. Five subgenera and 30 species are recognised in this scorpionid genus (Fet 2000). Four species, representing two of the Indian subgenera (*Chersonesometrus* Couzijn, 1981 and *Gigantometrus* Couzijn, 1981) and one of the South-East Asian subgenera (*Heterometrus* Ehrenberg, 1828) were included in this analysis to reflect variation in surface macrosculpture within the genus. *Heterometrus spinifer* is the type species. Couzijn (1981) suggested that *H. swammerdami* is the most basal species of the genus, based on outgroup comparison with *Pandinus*.

2. *Heterometrus fulvipes* (C. L. Koch, 1837). **India:** vi.1999, F. Somma, ♀ (AMCC 101695); Jeypore, ♀ (MCZ); Madireddy Palem, 1.i.1967, D. E. Johnson, 2 ♂, 3 ♀, 1 subad. ♂ (CAS).

3. *Heterometrus laoticus* Couzijn, 1981. **Laos:** vicinity of Vientiane, 28.iv.1965, L. G. Bush, ♂ (AMNH). **Vietnam:** Binh Dinh Province: Qui Nhon (Phutai), 5.viii.1965, L. J. Barrier, ♂ (CAS). **Thailand:** Doi Chang Dao, Asiatic Primate Exped., ♀ (MCZ). **Vietnam:** x.1997, D. Taylor, ♀ (AMCC 101697).

4. *Heterometrus spinifer* (Ehrenberg, 1828). **Malaysia:** Kuala Lumpur (Pahang Road), 2.v.1949, US Scrub Typhus Unit, 2 ♂ (USNM); Pulo Penang, vii.1860, W. H. A. Putnam, ♂, ♀ (MCZ). **Singapore:** ix.1998, K. Wee, ♂ (AMCC 101699).

5. *Heterometrus swammerdami* Simon, 1872. **India:** ix.2001, T. Gearheart, ♂ (AMCC 101700); Coimbatore, 2.vii.1954, P. Susai Nathan, ♂ (CAS); Periaculam, v.1963, Mrs D. C. Scudder, 2 ♂, 1 subad. ♀ (MCZ); Puttur Chittoor, xi.1952, E. Chell, ♂ (USNM). **Sri Lanka:** Western Province Chilaw, 13.v.1965, C. M. Bogert, ♂ (AMNH).

Opistophthalmus C. L. Koch, 1837. This is the largest scorpionid genus, with 59 described species (Prendini 2001*e*). The actual number is closer to 80 (L. Prendini, unpublished data). Four species were included in this analysis, to reflect the varied trichobothrial and carinal character states within the genus. Analysis of cladistic relationships among the species of *Opistophthalmus* (Prendini 2001*d*) suggests that the first species, which Kraepelin (1896) described as a species of *Heterometrus* and subsequently transferred to *Scorpio* (Kraepelin 1899), is relatively basal in the genus. The second species is the type species of *Opistophthalmus*. The third species was also originally described as a species of *Heterometrus*. The last species displays an array of derived psammophilous character states and was originally placed in a separate genus, *Protophthalmus*.

6. *Opistophthalmus boehmi* (Kraepelin, 1897). **South Africa:** Northern Province: Soutpansberg District: Farm Rochdale 700, E Waterpoort [22°54′S 29°42′E], i.1996, L. Prendini and J. Laing, ♂, ♀ (AMNH), 29.iii.1998, J. Leeming, ♀ (AMCC 100803).

7. *Opistophthalmus capensis* (Herbst, 1800). **South Africa:** Western Cape Province: Cape District: Oranjezicht, Cape Town, Table Mtn (northern slope) [33°56′S 18°25′E], 2.viii.1997, L. Prendini and E. Scott, ♂, ♀ (CAS), 1 juv. ♂ (AMCC 100811).

8. *Opistophthalmus carinatus* (Peters, 1861). **Namibia:** Khomas Region: Windhoek District: Farm Omdraai 114, E of Windhoek [22°44.00′S 17°47.67′E], 15.i.1998, L. Prendini and E. Scott, 1550 m, ♂ (NMNW 1927). **South Africa:** Northern Cape Province: Gordonia District: Kalahari Gemsbok Natl Pk: Nossob [25°25′S 20°36′E], 13.xii.1977, A. Harington, ♀ (AHC 628), xii.1992–i.1993, L. Prendini and K. M. A. Prendini, ♂ (SAMC C4819); Farm Alpha, 40 km S of Twee Rivieren on road to Andriesvale, ii.2001, J. du Plessis *et al.*, ♂ (AMCC 101708).

9. *Opistophthalmus holmi* (Lawrence, 1969). **Namibia:** Karas Region: Lüderitz District, Diamond Area 1: Namib-Naukluft Park: Koichab riverbed, dunes on northern bank [26°13.41′S 15°59.24′E], 3.ii.1998, L. Prendini, E. Scott and P. Swiegers, ♂, ♀ (AMNH), ♀ (AMCC 100846).

Pandinus Thorell, 1876. Five subgenera and 24 species (one of which has not been allocated to subgenus) are recognised in this scorpionid genus (Fet 2000). Four species, representing subgenera from western (*Pandinus* Thorell, 1876; *Pandinopsis* Vachon, 1974), central (*Pandinurus* Fet, 1997) and eastern Africa (*Pandinoides* Fet, 1997), were included in this analysis, to reflect the varied trichobothrial character states within the genus. *Pandinus imperator* is the type species. Vachon (1974) suggested that *P. dictator*, which he placed in a monotypic subgenus, is the most basal species in the genus.

10. *Pandinus cavimanus* (Pocock, 1888). **Kenya:** Tsavo, Taita Discovery Center, 27.iii.2000, R. Jocqué and C. Warui, 2 ♂ (MRAC 209.644, 210.006); Kikuyu, Dodoma, 21.xii.1929, A. Loveridge, 2 ♂, ♀ (MCZ); Mweru R., 13.viii.1909, S. M. Allen, ♀ (MCZ). **Tanzania:** xi.1997, F. Somma, 1 subad. ♂, 1 juv. ♀ (AMCC 101701).

11. *Pandinus dictator* (Pocock, 1888). **Cameroon:** Sassé, near Buea [04°09′N 09°14′E], *c.* 3500 ft on slope of Mt Cameroons, xii.1950, S. Tita, ♂, ♀ (CAS). **Gabon:** Prov. Ogooué-Maritime, Reserve de Faune de la Moukalaba-Dougoua, 12.2 km 305° NW Doussala, 02°17′S 10°29′E, 24.ii–3.iii.2000, B. L. Fisher, 110 m, 4 ♂, 2 ♀, juv. ♀ (CAS); Aire d'Exploit, Rationnelle de Faune des Monts Doudou, 24.3 km 307° NW Doussala, 02°13′S 10°24′E, 6–12.iii.2000, B. L. Fisher, ♀ (AMCC 101702).

12. *Pandinus imperator* (C. L. Koch, 1841). **Ghana:** xi.1997, D. Taylor, ♂ (AMCC 101703); Cape Coast [05°06′N 01°14′W], Univ. Cape Coast Collection, Dr Jerry Boggs, ♂, ♀, 5 juv. (AMNH). **Liberia:** Nimba County, Oldtown Gobonwea, 225 mi from Monrovia, 40 mi E Mt Nimba [07°33′N 08°37′W], C. D. Miller III, 2 ♂, 2 ♀ (AMNH), 4 ♂, 3 ♀ (USNM).

13. *Pandinus viatoris* (Pocock, 1890). **Democratic Republic of Congo:** Lukafu, 6–22.xii.1930, G. F. de Witte, ♀, 1 subad. ♂, 1 juv. ♀ (MRAC 023.806). **Zambia:** Fort Jameson, V. J. Wilson, ♂, ♀ (NMSA); Chief Sayiri Area, 30 mi from Fort Jameson, 6–18.i.1964, 2 ♂, 1 subad.

♂, 1 subad. ♀, 1 juv. ♀ (NMSA); Mpulungu, 1994, P. D. Plisnier, ♂ (MRAC 209.525). **Tanzania:** xii.1993, M. Scharmach, ♂ (AMCC 101704).

Scorpio Linnaeus, 1758. A single species, with 19 subspecies (Fet 2000), is currently recognised in this scorpionid genus. The two subspecies included in this analysis represent extremes in the morphological variation subsumed into this monotypic species and may be viewed as phylogenetic species (Nelson and Platnick 1981; Cracraft 1983, 1989; Wheeler and Nixon 1990; Nixon and Wheeler 1990).

14. *Scorpio maurus fuscus* (Ehrenberg, 1829). **Israel:** vi.1998, Y. Lubin, 1 subad. ♂ (AMCC 101705); Bet-Guvzin, 27.iii.1967, N. Roman, ♂ (AMNH); Jerusalem, 25.vii.1961, P. Amitai, ♀ (AMNH); Palestine, Afule, 25.ix.1934, Dr F. R. S. Shaw, 5 ♀, 2 subad. ♂, 2 juv. ♀ (FMNH). **Lebanon:** Beirut, campus of American University of Beirut, 23.x.1961, A. J. Sam, 2 ♀, 1 juv. ♀ (CAS).

15. *Scorpio maurus palmatus* (Ehrenberg, 1828). **Egypt:** x.1997, D. Taylor, ♀ (AMCC 101706); Cairo, 1.x.1954, Capt. E. L. Amiriya, US Nat. Med. Res. Unit, Wells and Randall, ♀ (USNM). **Israel:** S. A. Minton, ♀ (AMNH).

Appendix 2. Characters, states and optimisations in cladistic analysis of the family Scorpionidae

Character states were scored 0, 1, 2, 3, ? (unknown) or – (inapplicable). Multistate characters were treated as unordered (nonadditive). Refer to Table 3 for data matrix. Terminology follows Vachon (1974) for trichobothrial notation, Couzijn (1976) for segmentation of legs, Hjelle (1990) and Sissom (1990) for segmentation of pedipalps, Prendini (2000*a*) for pedipalp and metasomal carinae, and Stahnke (1970), Lamoral (1979), Couzijn (1981) and Sissom (1990) for remaining features. Characters corresponding to the lists of Lamoral (1979: table 6), Couzijn (1981: tables 2 and 9) and Prendini (2000*a*: appendix 3) are denoted, respectively, by the abbreviations BHL, HWC and LP, followed by the corresponding number. Character optimisations are based on the optimal tree obtained in the present investigation. Ambiguous optimisations were mostly resolved with ACCTRAN, but DELTRAN was also used in some cases. Five uninformative characters (excluded from all analyses) are indicated by †.

Overall size

1. *Adult length, measured from anterior margin of carapace to tip of aculeus*: medium, minimum length of 50 mm to maximum length of 120 mm (0); extremely large, minimum length >120 mm (1). Extreme size is apomorphic in the Scorpionidae and evolved at least twice in the family: in *H. swammerdami* and in the West African *Pandinus* (including *P. dictator* and *P. imperator*).

Chelicerae

2. *Cheliceral movable finger, distal external and distal internal teeth*: subequal, with distal external tooth only slightly smaller than distal internal tooth, and opposable, that is, forming a bicusp (0); unequal, with distal external tooth considerably smaller than distal internal tooth, aligned longitudinally and usually not opposable or, at most, moderately opposable (1). [LP 11] By comparison with the diplocentrid outgroup, unequal, longitudinally aligned distal teeth are synapomorphic for the Scorpionidae, but have reversed to the plesiomorphic subequal, opposable condition at least twice in the family: in the West African *Pandinus* (including *P. dictator* and *P. imperator*) and in the South-East Asian *Heterometrus* (including *H. laoticus* and *H. spinifer*).

3. *Cheliceral coxae, scaphotrix (stridulatory setae) on dorso-internal surfaces*: absent (0); present (1). [LP 13] The presence of scaphotrix on the dorsointernal surfaces of the cheliceral coxae is synapomorphic for *Opistophthalmus*.

4. *Cheliceral coxae, trichocopae (chemoreceptive lamelliform setae) on internal surfaces*: absent (0); present (1). [LP 14] The presence of trichocopae on the internal surfaces of the cheliceral coxae is also synapomorphic for *Opistophthalmus* and, of the species included in this analysis, observed in *O. boehmi*, *O. carinatus* and *O. capensis*. Reversals to plesiomorphic absence occur in more derived species of the genus (e.g. *O. holmi*).

Carapace

5. *Median notch in anterior margin*: strongly excavated (0); shallow (1). [LP 3] A shallowly excavated median notch was previously considered to be synapomorphic for (*Opistophthalmus* + *Scorpio*) (Prendini 2000*a*). However, on the basis of the present reconstruction, it either evolves independently in the two genera (DELTRAN), or represents a synapomorphy for the Scorpionidae, with a reversal to the plesiomorphic, strongly excavated condition in (*Pandinus* + *Heterometrus*) (ACCTRAN).

6. *Median notch or anterior median depression with median lobe projecting anteriorly*: absent (0); present (1). As reconstructed under ACCTRAN, the presence of a median lobe is synapomorphic for some species of *Opistophthalmus* (e.g. *O. carinatus* and *O. capensis*). However, a reversal to plesiomorphic absence occurs in other, more derived species of the genus (e.g. *O. holmi*).

7. *Anterior median depression*: absent (0); present (1). The anterior median depression is synapomorphic for most derived species of *Opistophthalmus* (including *O. carinatus*, *O. capensis* and *O. holmi*).

8. *Anterocular depression*: absent, distal portions of superciliary carinae parallel (0); present, distal portions of superciliary carinae subparallel or diverging (1). The presence of an anterocular depression is synapomorphic for *Opistophthalmus*.

9. *Circumocular depressions*: converging distally (0); diverging distally (1). Distally diverging circumocular depressions are synapomorphic for most derived species of *Opistophthalmus* (including *O. carinatus*, *O. capensis* and *O. holmi*).

10. *Position of median ocular tubercle, expressed as the ratio of distance from anterior margin of carapace to median ocular tubercle*:*carapace length*: anteromedial, 0.40–0.50 (0); posteromedial, 0.51–0.62 (1); distinctly posterior, 0.63–0.78 (2). [Modified BHL 3: merged states 2 and 3.] By comparison with the diplocentrid outgroup, the posteromedial position of the ocular tubercle is synapomorphic for the Scorpionidae, but has reversed to the plesiomorphic, anteromedial position in some species of *Opistophthalmus* (e.g. *O. holmi*). The ocular tubercle has also become more posteriorly displaced in other species of *Opistophthalmus* (e.g. *O. capensis*).

11. *Superciliary carinae*: with anterocular extensions (0); without anterocular extensions (1). [Incorporating HWC 7.] The presence of anterocular extensions of the superciliary carinae is plesiomorphic in *O. boehmi* and *Heterometrus*, by comparison with the diplocentrid outgroup (DELTRAN). Absence thereof has evolved on three independent occasions in the Scorpionidae: in most derived *Opistophthalmus* (including *O. carinatus*, *O. capensis* and *O. holmi*), in *Pandinus*, and in *Scorpio*.

12. *Superciliary carinae*: higher than median ocelli (0); lower than median ocelli (1). [Merged BHL 9 and 10.] Weakly developed superciliary carinae, lower than the median ocelli, have evolved independently in *Scorpio*, and in some derived species of *Opistophthalmus* (e.g. *O. capensis* and *O. holmi*).

13. *Rostrolateral margin of carapace*: with distinct incision next to posterior lateral ocelli (0); entire (1). [Mentioned by Couzijn (1981) but not listed in his table 2.] Rostrolateral incisions have evolved at least twice in the Scorpionidae: in some South-East Asian *Heterometrus*

(e.g. *H. laoticus* and *H. spinifer*) and in some East African *Pandinus* (e.g. *P. cavimanus* and *P. viatoris*).

14. *Interocular suture*: slender (0); broad (1); absent (2). A broadened interocular suture is synapomorphic for most derived species of *Opistophthalmus* (including *O. carinatus* and *O. capensis*), but the interocular suture has also been lost in some derived members of the genus (e.g. *O. holmi*).

15. *Posterior sutures, configuration*: extending from posterior carapace margin to median ocular tubercle (0); extending from posterior carapace margin, anteriorly past median ocular tubercle (1); absent (2). Posterior sutures, extending past the ocular tubercle, evolved on at least three independent occasions in the Scorpionidae: in basal *Opistophthalmus* (e.g. *O. boehmi*), in some East African *Pandinus* (e.g. *P. cavimanus* and *P. viatoris*), and in some Indian *Heterometrus* (e.g. *H. fulvipes* and *H. swammerdami*). Posterior sutures have been lost in some derived *Opistophthalmus* (e.g. *O. holmi*).

16. *Posterior sutures, configuration*: connected distally to posterior furcations of interocular suture (0); regardless of the presence or absence of interocular suture, posterior sutures connected by short cross-suture anterior to postocular depression (1); absent (2). The presence of a short cross-suture immediately anterior to the postocular depression is synapomorphic for some derived species of *Opistophthalmus* (e.g. *O. carinatus* and *O. capensis*), but this suture has also been lost in other derived members of the genus (e.g. *O. holmi*).

17. *Interocular surface, macrosculpture, distribution (♂)*: entirely smooth (0); granular along median longitudinal and anterior furcated sulci only (1); frontal lobes and median region granular, with smooth areas (2); entire surface uniformly granular (3). [Modified BHL 4 by adding two states to account for variation in the distribution of granulation.] As reconstructed under DELTRAN, the presence in ♂ of granulation along the median longitudinal and anterior furcated sulci only is plesiomorphic in some species of *Opistophthalmus* (e.g. *O. carinatus* and *O. capensis*) and *Heterometrus* (e.g. *H. fulvipes* and *H. spinifer*). Further loss of granulation, to an entirely smooth interocular surface as in *H. laoticus*, is apomorphic, as is the progressive increase in granulation, from the frontal lobes and median region in *O. boehmi*, *O. holmi*, *H. swammerdami* and the East African exemplars of *Pandinus* (*P. cavimanus* and *P. viatoris*), to the entire surface in *Scorpio* and the West African exemplars of *Pandinus* (*P. dictator* and *P. imperator*).

18. *Interocular surface, macrosculpture, distribution (♀)*: entirely smooth (0); granular along median longitudinal and anterior furcated sulci only (1); frontal lobes and median region granular, with smooth areas (2); entire surface uniformly granular (3). [Modified BHL 5 by adding two states to account for variation in the distribution of granulation.] The complete absence of granulation on the interocular surface in ♀ is plesiomorphic in *Scorpio*, on the basis of its occurrence in the diplocentrid outgroup (DELTRAN). Granulation along the median longitudinal and anterior furcated sulci only is apomorphic in some species of *Opistophthalmus* (e.g. *O. carinatus* and *O. capensis*) and *Heterometrus* (e.g. *H. fulvipes* and *H. spinifer*), as is the progressive increase in granulation, from the frontal lobes and median region in *O. boehmi*, *H. swammerdami*, *P. imperator* and *P. viatoris*, to the entire surface in *P. dictator*. Three independent reversals to the plesiomorphic, entirely smooth interocular surface occur in the following exemplars: *O. holmi*, *P. cavimanus*, *H. laoticus*.

19. *Anterolateral surfaces, macrosculpture (♀)*: granular (0); smooth or nearly so (1). [Part of BHL 6.] Smooth anterolateral surfaces in ♀ are apomorphic, and evolved independently in some *Opistophthalmus* (e.g. *O. holmi*) and South-East Asian *Heterometrus* (e.g. *H. laoticus* and *H. spinifer*).

20. *Posteromedian surface, macrosculpture (♂)*: granular (0); smooth or nearly so (1). [BHL 7] A smooth posteromedian surface in ♂ is synapomorphic for (*Pandinus* + *Heterometrus*) and evolved independently in some *Opistophthalmus* (e.g. *O. holmi*).

Pedipalps

21. †*Femur, length (♀), expressed as ratios of femur length : posterior carapace width (fl : pcw) and femur length : carapace length (fl : cl)*: long, fl : pcw < 0.77, fl : cl < 0.74 (0); short, fl : pcw ≥ 0.80, fl : cl ≥ 0.76 (1). [Surrogate for BHL 16, which could not be applied objectively.] A short femur represents a potential synapomorphy for the Scorpionidae, by comparison with the diplocentrid outgroup in which a long femur is present, but the character is uninformative in the present analysis. The apomorphic state also occurs in some derived species of *Opistophthalmus* (not included in the analysis).

23. *Chela fingers, terminal teeth interlocking when closed*: evenly, movable finger not displaced to exterior (0); unevenly, movable finger displaced to exterior, with weakly developed notch near tip of fixed finger (1); unevenly, movable finger displaced to exterior, with strongly developed notch near tip of fixed finger (2). Unevenly interlocking terminal teeth are synapomorphic for the Scorpionidae, by comparison with the diplocentrid outgroup. A weakly developed notch near the fingertip, as observed in *Opistophthalmus* and *Scorpio*, represents the more plesiomorphic state of this transformation series. The more pronounced notch is further derived, and synapomorphic for (*Pandinus* + *Heterometrus*).22. Chela, macrosetal development (adult ♂): virtually asetose (0); sparsely setose (1); moderately to densely setose (2). By comparison with the diplocentrid outgroup, a sparsely setose chela in the adult ♂ is synapomorphic for the Scorpionidae, but only *Scorpio* and *Heterometrus* exhibit this state. Increased setation of the chela, as observed in *Pandinus* and *Opistophthalmus* (with a reversal to the sparsely setose condition in some species, e.g. *O. holmi*), is further derived.

24. *Chela movable finger, basal lobe (♂)*: arising gradually from base of finger, leaving a small to large gap behind when fingers are closed (0); arising abruptly from base of finger, without leaving gap behind when fingers are closed (1). As reconstructed under DELTAN, an abruptly arising basal lobe on the movable finger of the ♂ is apomorphic and evolved independently on more than one occasion in *Opistophthalmus* (e.g. in *O. carinatus* and *O. holmi*).

25. *Chela movable finger, second lobe (♂)*: more strongly developed than other lobes on the movable finger, with correspondingly well-developed notch in fixed finger (0); not noticeably larger or only slightly larger than other lobes on the movable finger (1). [Modified LP 35: state 0 now also recognised in *Nebo*.] By comparison with the diplocentrid outgroup, a weakly developed second lobe on the movable finger of the ♂ evolved is synapomorphic for the Scorpionidae. A reversal to the plesiomorphic, strongly developed condition is synapomorphic for (*Pandinus* + *Heterometrus*), while a reversal occurred independently in *O. carinatus*.

26. *Chela fingers, surface macrosculpture*: smooth (0); granular (1). Granular chela fingers are synapomorphic for (*Pandinus* + *Heterometrus*), but evolved independently in a few derived species of *Opistophthalmus* (e.g. *O. holmi*).

27. *Chela manus, dorsomedian carina, posteromarginal portion*: present (0); absent (1). Absence of the posteromarginal portion of the chela dorsomedian carina evolved at least twice in the Scorpionidae: in some East African *Pandinus* (e.g. *P. cavimanus* and *P. viatoris*) and some South-East Asian *Heterometrus* (e.g. *H. laoticus* and *H. spinifer*).

28. *Chela manus, dorsal surface, macrosculpture (♀)*: smooth (0); finely to coarsely granular (1). [State 1 of BHL 17 and 18. Incorporates HWC 60 and 61.] By comparison with the diplocentrid outgroup, a granular dorsal surface of the chela manus in the ♀ is synapomorphic for the Scorpionidae, but reversed to the plesiomorphic smooth condition at least twice in the family: in some East African *Pandinus* (e.g. *P. cavimanus* and *P. viatoris*) and some South-East Asian *Heterometrus* (e.g. *H. laoticus* and *H. spinifer*).

29. *Chela manus, dorsal surface, macrosculpture (♂)*: shallowly reticulate (0); reticulation absent (1). [State 0 of BHL 17. Incorporates

HWC 61.] Absence of reticulation on the dorsal surface of the chela manus in ♂ is synapomorphic for the Scorpionidae, but reversed to the plesiomorphic reticulate condition in some East African *Pandinus* (e.g. *P. cavimanus* and *P. viatoris*).

30. *Chela manus, dorsal surface, macrosculpture (♀)*: shallowly reticulate (0); reticulation absent (1). [State 0 of BHL 18. Incorporates HWC 61.] Absence of reticulation on the dorsal surface of the chela manus in ♀ is synapomorphic for the Scorpionidae, but reversed to the plesiomorphic reticulate condition in some East African *Pandinus* (e.g. *P. cavimanus* and *P. viatoris*) and, independently, in some species of *Opistophthalmus* (e.g. *O. carinatus*).

31. *Chela manus, dorsal secondary and subdigital carinae (♂)*: absent or obsolete (0); entirely to predominantly granular (1). [Incorporates HWC 61.] Granular dorsal secondary and subdigital carinae of the chela manus are synapomorphic for *Scorpio* but evolved independently in some species of *Opistophthalmus* (not included in the analysis).

32. *Chela manus, digital carina*: entirely to predominantly costate (0); entirely to predominantly granular (1); absent or obsolete (2). [Merged BHL 19 and 20 because these have the same distribution and do not appear to be independent.] A strong, costate digital carina is plesiomorphic in the Scorpionidae, on the basis of its occurrence in the diplocentrid outgroup. As reconstructed under DELTRAN, a weak, granular digital carina evolved at least twice in the family: in *Scorpio* and in some species of *Opistophthalmus* (e.g. *O. boehmi*). Reduction or loss of the digital carina evolved independently in (*Pandinus* + *Heterometrus*) and some *Opistophthalmus* (e.g. *O. holmi*).

33. *Chela manus, external intercarinal surfaces, macrosculpture (♂)*: granular (0); smooth or nearly so (1). Loss of granulation on the external intercarinal surfaces of the chela manus in ♂ is synapomorphic for some South-East Asian *Heterometrus* (e.g. *H. laoticus* and *H. spinifer*) and evolved independently in some species of *Opistophthalmus* (e.g. *O. capensis*).

34. *Chela manus, external intercarinal surfaces, macrosculpture (♀)*: granular (0); smooth or nearly so (1). Loss of granulation on the external intercarinal surfaces of the chela manus in ♀ is synapomorphic for some South-East Asian *Heterometrus* (e.g. *H. laoticus* and *H. spinifer*).

35. *Chela manus, internomedian carina (♀)*: present, granular (0); absent or obsolete (1). Reduction or loss of the internomedian carina in ♀ is synapomorphic for some derived species of *Opistophthalmus* (e.g. *O. capensis* and *O. holmi*).

36. †*Chela manus, ventrointernal carina (♀)*: more strongly developed than internomedian carina, which may be obsolete (0); equally developed (1); absent (2). [LP 29 with the addition of state 2.] Equal or reduced development of the ventrointernal carina, relative to the internomedian carina, is plesiomorphic in the Scorpionidae, the alternative condition being apomorphic in *Nebo* (Prendini 2000*a*). Absence of the ventrointernal carina is synapomorphic for a few derived species of *Opistophthalmus* (e.g. *O. holmi*), but this character is uninformative in the present analysis.

37. *Chela manus, ventromedian carina*: absent or reduced to a few proximal granules (0); present and strongly sclerotised (1); present and weakly sclerotised (2). [Modified LP 28 with a new state to distinguish between weak or strong sclerotisation of the ventromedian carina.] A strongly sclerotised ventromedian carina is synapomorphic for the Scorpionidae, by comparison with the outgroup diplocentrid, in which a vestigial ventromedian carina is present. Reduced sclerotisation of the ventromedian carina is synapomorphic for (*Pandinus* + *Heterometrus*) and evolved independently in several species of *Opistophthalmus* (e.g. *O. boehmi* and *O. holmi*).

38. †*Patella, dorsal surface, shape*: flat (or nearly so), dorsomedian and dorsoexternal carinae in same axis (0); convex, dorsomedian carina raised above horizontal axis of dorsoexternal carina (1). [LP 15] A convex patella is synapomorphic for the Scorpionidae, although it reversed in some *Opistophthalmus* (not included in the analysis). This character is uninformative in the present analysis.

39. *Patella, dorsomedian carina (♀)*: entirely to predominantly granular (0); entirely to predominantly costate (1); absent or obsolete (2). As reconstructed under ACCTRAN, a costate dorsomedian carina in the ♀ is synapomorphic for some derived species of *Opistophthalmus* (e.g. *O. carinatus* and *O. capensis*), but reversed to the granular condition in other derived members of the genus (e.g. *O. holmi*). The costate condition evolved independently in some *Scorpio* (e.g. *S. maurus fuscus*). Reduction or loss of the dorsomedian carina is synapomorphic for (*Pandinus* + *Heterometrus*).

40. *Patella, dorsal intercarinal surfaces, macrosculpture (♀)*: granular (0); smooth or nearly so (1). [HWC 37] Smooth dorsal intercarinal surfaces in the ♀ are synapomorphic for (*Scorpio* + *Pandinus* + *Heterometrus*), and evolved independently in some species of *Opistophthalmus* (e.g. *O. capensis*). A reversal to the plesiomorphic granular condition occurs in some Indian *Heterometrus* (e.g. *H. fulvipes* and *H. swammerdami*).

41. *Patella, dorsoexternal and ventroexternal intercarinal surfaces, macrosculpture (♀)*: granular (0); smooth or nearly so (1). [Merged BHL 32 and 33 because of identical distributions. Incorporates HWC 37.] Smooth dorsoexternal and ventroexternal intercarinal surfaces in the ♀ are synapomorphic for (*Scorpio* + *Pandinus* + *Heterometrus*) and evolved independently in some species of *Opistophthalmus* (e.g. *O. capensis*). A reversal to the plesiomorphic granular condition occurs in some Indian *Heterometrus* (e.g. *H. fulvipes* and *H. swammerdami*).

42. *Patella, dorsoexternal carina (♀)*: absent or obsolete (0); as strongly developed as, or more strongly developed than, externomedian carinae (1). A strongly developed dorsoexternal carina in the ♀ is synapomorphic for (*Pandinus* + *Heterometrus*), but reverses to plesiomorphic absence in some Indian *Heterometrus* (e.g. *H. fulvipes* and *H. swammerdami*). A strongly developed dorsoexternal carina evolved independently in several species of *Opistophthalmus* (e.g. *O. carinatus*).

43. *Patella, paired externomedian carinae (♀)*: granular or costate (0); absent or obsolete (1). Reduction or loss of the paired externomedian carinae in the ♀ is synapomorphic for (*Pandinus* + *Heterometrus*).

44. *Femur, dorsoexternal carina*: less strongly developed than dorsointernal carina (0); more strongly developed than dorsointernal carina (1). [Modified HWC 28. Corrected entries for *Opistophthalmus*.] Increased development of the dorsoexternal carina, compared with the dorsointernal carina, is also synapomorphic for (*Pandinus* + *Heterometrus*).

45. *Femur, dorsointernal carina*: present and distinct (0); absent or obsolete (1). Reduction or loss of the dorsointernal carina is synapomorphic for *Pandinus*, and also for a few derived species of *Opistophthalmus* (e.g. *O. holmi*).

46. *Femur, internomedian carina*: oriented parallel to dorsointernal and ventrointernal carinae (0); oriented diagonally across from ventrointernal carina to dorsointernal carina (1). By comparison with the diplocentrid outgroup, a diagonal orientation of the internomedian carina, relative to the dorsointernal and ventrointernal carinae, is synapomorphic for the Scorpionidae, but has reversed to the plesiomorphic, parallel orientation in several species of *Opistophthalmus* (e.g. *O. carinatus*).

47. *Femur, ventroexternal carina (♂)*: absent or obsolete (0); present (1). The presence of a ventroexternal carina on the femur is synapomorphic for *Opistophthalmus*, but has reversed to plesiomorphic absence in a few derived species of *Opistophthalmus* (e.g. *O. holmi*).

48. *Stridulatory organ on opposing surfaces of coxae of pedipalps and first walking legs*: absent (0); weakly developed (1); well developed (2). [LP 74] The presence of a stridulatory organ on opposing coxal surfaces of the pedipalps and first walking legs is synapomorphic for (*Scorpio* + *Pandinus* + *Heterometrus*), while a fully developed stridulatory organ represents a further derivation, synapomorphic for (*Pandinus* + *Heterometrus*).

49. *Stridulatory organ on opposing surfaces of coxae of pedipalps and first walking legs*: absent (0); granular tubercles of 'rasp' and stridulatory setae (scaphotrix) of 'scraper' situated on coxae of pedipalp and first leg, respectively (1); granular tubercles of 'rasp' and stridulatory setae (scaphotrix) of 'scraper' situated on coxae of first leg and pedipalp, respectively (2). [LP 75] The rasp–scraper configuration on the coxae of first leg and pedipalp is synapomorphic for *Heterometrus*, and derived from the configuration observed in *Scorpio* and *Pandinus*, where the relative positions of the rasp and scraper are reversed.

Trichobothria (τ)

50. *Chela, distance* est–esb: greater than half distance *esb–eb* (0); *c.* half distance *esb–eb* (1). [Merged BHL 23 and 24 because these have the same distribution.] The halved distance between *esb* and *eb* is synapomorphic for the South-East Asian *Heterometrus* (including *H. laoticus* and *H. spinifer*), and under ACCTRAN, for some species of *Opistophthalmus* (e.g. *O. carinatus* and *O. capensis*). Reversals to the plesiomorphic distance have occurred in other species of *Opistophthalmus* (e.g. *O. holmi*).

51. *Chela, number of* V τ: 4 (0); 8–10 (1); 15–20 (2). [Modified BHL 26 and LP 49 with extra states recognised.] Accessory trichobothria in the *V* series are apomorphic in the Scorpionidae, occurring in most species of *Pandinus* (only *P. dictator* exhibits 4 *V* trichobothria) and in a few species of *Opistophthalmus* (e.g. *O. holmi*). The occurrence of 4 *V* trichobothria in *P. dictator* may be interpreted as plesiomorphic in the genus (ACCTRAN), or as a reversal to the plesiomorphic number (DELTRAN).

52. *If only 4* V τ*, longitudinal position of* τ V_3 *on chela manus*: distal third (0); proximal third (1); inapplicable (–). [BHL 25 with state for *Nebo* and *P. dictator*.] The proximal position of V_3 is synapomorphic for the Scorpionidae, by comparison with the diplocentrid outgroup, while the distal position of V_3 in *P. dictator* constitutes a reversal to the plesiomorphic, distal position. This character is inapplicable in the taxa with more than 4 *V* trichobothria.

53. *Chela, number of* i τ: 2 (0); 3 or 4 (1). [LP 46] Accessory trichobothria in the *i* series are apomorphic in the Scorpionidae, occurring in many species of *Pandinus*. Among the exemplars included in the present analysis, more than 2 *i* trichobothria evolved independently in *P. cavimanus* and *P. imperator*.

54. *Patella, number of* e τ: 13 (0); 14 (1); 16 (2); 24–31 (3). [Modified BHL 27 and LP 45 with extra states recognised.] Accessory trichobothria in the *e* series are apomorphic in the Scorpionidae, and evolved independently in *Opistophthalmus* and *Pandinus*, all species of which have more than 13 *e* trichobothria. Several species of *Opistophthalmus* (e.g. *O. holmi*) and *Pandinus* (e.g. *P. imperator*) exhibit more than 14 *e* trichobothria, these states being further derived.

55. *Patella, number of* v τ: single row of 3 (0); single row of 4–13 (1); two or more rows of >25 (2). [Modified BHL 28 and LP 43 with extra states recognised.] Accessory trichobothria in the *v* series are apomorphic in the Scorpionidae, and also evolved independently in *Opistophthalmus* and *Pandinus*. However, whereas relatively few species of *Opistophthalmus* (e.g. *O. holmi*) exhibit a single row of more than 3 *v* trichobothria, two or more rows of >25 *v* trichobothria is synapomorphic for *Pandinus*.

56. *Femur, position of* τ i: internal surface (0); dorsal surface. [LP 40] The dorsal position of trichobothrium *i* on the femur is synapomorphic for *Scorpio*.

Genitalia

57. *Genital opercula (♂)*: not overlapping (0); overlapping (1). Overlapping genital opercula in the ♂ are synapomorphic for (*Pandinus* + *Heterometrus*).

58. †*Hemispermatophore, distal crest of distal lamina*: tapering, diplocentrid type (0); truncate (1); tapering, scorpionid type (2). [Mentioned by Lamoral (1978*b*, 1979) but not listed as a character.] A truncate distal crest of the distal lamina is plesiomorphic in the Scorpionidae, the alternative condition being apomorphic in the Diplocentridae. A tapering distal crest (not homologous with that observed in the diplocentrids) is synapomorphic for two derived species of *Opistophthalmus*, only one of which (*O. holmi*) was included in the present analysis. This character is therefore uninformative.

59. *Hemispermatophore, with well-developed accessory distal lobe protruding between articular suture and distal lobe (hook)*: absent (0); present (1). [Mentioned by Couzijn (1981) but not listed in his table 2.] An accessory distal lobe of the hemispermatophore is synapomorphic for *Heterometrus*.

Pectines

60. *Pecten length, expressed relative to length of coxa of leg IV (♂)*: long, distal edge reaching beyond distal edge of coxa (0); moderate, distal edge reaching to, but not beyond, distal edge of coxa (1); short, distal edge not reaching to distal edge of coxa (2). By comparison with the diplocentrid outgroup, long pectines are plesiomorphic in the Scorpionidae, occurring only in basal *Opistophthalmus* (e.g. *O. boehmi* and *O. carinatus*). Reduction in pectinal length is synapomorphic for (*Scorpio* + *Pandinus* + *Heterometrus*), but also evolved independently in derived *Opistophthalmus* (e.g. *O. capensis*), in which a further reduction occurred in several species (e.g. *O. holmi*).

61. *First proximal median lamella (scape), angle (♂)*: approximately 90° (0); obtuse, >90° but <180° (1). An obtuse pectinal scape in the ♂ is synapomorphic for (*Scorpio* + *Pandinus* + *Heterometrus*), but evolved independently in several *Opistophthalmus* (e.g. *O. holmi*).

62. *First proximal median lamella (scape), angle (♀)*: distinctly angular, >90° but <180° (0); straight or shallowly curved (1). A straight or shallowly curved pectinal scape in the ♀ evolved independently in several species of *Opistophthalmus* (e.g. *O. boehmi* and *O. holmi*) and *Pandinus* (e.g. *P. cavimanus*).

63. *Pectinal teeth, shape (♂)*: short, curved (0); long, straight (1). Long, straight pectinal teeth are synapomorphic for (*Pandinus* + *Heterometrus*) and evolved independently in some species of *Opistophthalmus* (e.g. *O. boehmi*).

64. *Internal fulcral plates, setation*: smooth to sparsely setose (three or four microsetae distally) (0); smooth proximally but densely setose (microsetae only) distally (1); sparsely setose (scattered macrosetae) across entire surface (2). [Modified HWC 86. Redefined states.] By comparison with the diplocentrid outgroup, proximally smooth but distally setose fulcral plates are synapomorphic for the Scorpionidae. Entirely but sparsely setose fulcral plates are relatively derived, and evolved independently in *Opistophthalmus* and *Scorpio* (ACCTRAN or DELTRAN).

Legs

65. *Femora, ventromedian surfaces*: acarinate, no discernible carina demarcating prolateral and retrolateral surfaces (0); unicarinate, distinct prolateral and retrolateral surfaces marked by macrosetae and, usually, granules (1); bicarinate, distinct ventromedian surface as well as prolateral and retrolateral surfaces marked by macrosetae and usually granules, although prolateral carinae often weakly developed (2). Unicarinate ventromedian surfaces are synapomorphic for the Scorpionidae, by comparison with the diplocentrid outgroup. Bicarinate ventromedian surfaces are synapomorphic for (*Pandinus* + *Heterometrus*).

66. *Tibiae I and II, retrolateral margin, setation*: no macrosetae (0); a row of spiniform macrosetae only (1); a comb-like row of setiform macrosetae (2). A row of spiniform macrosetae on the retrolateral margins of tibiae I and II is synapomorphic for the Scorpionidae, but reverses to the plesiomorphic absence of macrosetae in *Heterometrus*. A comb-like row of setiform macrosetae has evolved in many species of *Opistophthalmus* (e.g. *O. capensis* and *O. holmi*).

67. *Basitarsi I and II, retrolateral margin, setation*: no macrosetae (0); a row of three or more spiniform macrosetae (1); a row of only two spiniform macrosetae (2); a comb-like row of three or more setiform macrosetae that may or may not be interspersed with slender spiniform macrosetae (3). [Modified BHL 76; merged LP 72 and 73.] By comparison with the diplocentrid outgroup, a row of three or more spiniform macrosetae on the retrolateral margins of basitarsi I and II is synapomorphic for the Scorpionidae. A reduction in the number of macrosetae from three or more to two is synapomorphic for (*Pandinus* + *Heterometrus*). A comb-like row of three or more setiform macrosetae has evolved in many species of *Opistophthalmus* (e.g. *O. capensis* and *O. holmi*).

69. *Telotarsi, laterodistal lobes, setation*: three or more spiniform macrosetae on each laterodistal lobe (0); only two spiniform macrosetae on each laterodistal lobe (1). A reduction in the number of spiniform macrosetae on the laterodistal lobes is synapomorphic for (*Pandinus* + *Heterometrus*).68. Telotarsi, shape in dorsal and lateral views: type I, short, stout, distally broadened in dorsal and especially lateral view (0); type II, long, narrow, parallel-sided in dorsal and lateral views (1). As reconstructed under ACCTRAN, type II telotarsi are synapomorphic for *Opistophthalmus*, occurring in relatively basal species of the genus (e.g. *O. boehmi* and *O. carinatus*). However, a reversal to plesiomorphic type I telotarsi occurs in derived *Opistophthalmus* (e.g. *O. capensis* and *O. holmi*).

70. *Telotarsi, number of spiniform macrosetae in prolateral row*: constant or increasing from telotarsi I–IV (0); constant or increasing from telotarsi I–III, but decreasing on telotarsus IV (1). A decreasing count of spiniform macrosetae in the prolateral rows of the telotarsi occurs in many species of *Opistophthalmus*. As reconstructed under DELTRAN, decreasing counts evolved independently in *O. boehmi* and (*O. capensis* + *O. holmi*).

71. *Telotarsi, prolateral row of spiniform macrosetae (excluding macrosetae on laterodistal lobes)*: present on telotarsi I–IV (0); present on telotarsi I–III, absent on telotarsus IV (1); absent on telotarsi I–IV (2). [Incorporates BHL 77 and 79, LP 71.] Progressive loss of the prolateral rows of spiniform macrosetae on the telotarsi occurs in many species of *Opistophthalmus*. As reconstructed under DELTRAN, *O. boehmi* and *O. holmi* each represent an independent loss of the prolateral row. However, in *O. holmi*, this state transforms from the intermediate state in *O. capensis*, in which the prolateral row is lost only on telotarsus IV, whereas in *O. boehmi*, the transformation occurs directly from the plesiomorphic state.

72. *Telotarsi, ungues, shape*: short and distinctly curved (0); elongated and weakly curved (proximally or distally) to sublinear (1). [Modified BHL 82.] Elongated, weakly curved to sublinear telotarsal ungues evolved in many species of *Opistophthalmus* (e.g. *O. capensis* and *O. holmi*).

73. *Telotarsi, ungues, relative length within each pair*: equal to subequal on telotarsi I–IV (0); unequal on telotarsi I and II, equal to subequal on telotarsi III and IV (1). [Merged BHL 83 and 84.] Unequal development of the telotarsal ungues occurs in most species of *Opistophthalmus*, and is synapomorphic for the genus.

Tergites

74. *Tergites I–VI, surface macrosculpture, distribution (♂)*: mesial and lateral surfaces granular (0); mesial surfaces smooth, lateral surfaces granular (rarely smooth) (1). [Modified BHL 34, states 0, 1 and 2. Incorporates HWC 91.] Absence of granulation on the mesial surfaces of tergites I–VI in the ♂ is synapomorphic for most South-East Asian *Heterometrus* (including *H. laoticus* and *H. spinifer*).

75. *Tergites I–VI, surface macrosculpture, distribution (♀)*: mesial and lateral surfaces smooth (0); mesial surfaces granular, lateral surfaces smooth (1); mesial and lateral surfaces granular (2). [HWC 91] The presence of granulation on the mesial surfaces of tergites I–VI in the ♀ is synapomorphic for most South-East Asian *Heterometrus* (including *H. laoticus* and *H. spinifer*) and, independently, for *Opistophthalmus* (ACCTRAN). The presence of granulation on both the mesial and lateral surfaces of tergites I–VI in the ♀ is further derived in some species of *Opistophthalmus* (e.g. *O. capensis*).

76. *Tergites I–VI, surface macrosculpture, texture (♂)*: uniformly finely granular (0); unevenly finely and coarsely granular to predominantly coarsely granular (1). [BHL 34, states 1 and 2, with state 0 transferred to another character.] Coarse granulation of the tergites in the ♂ is synapomorphic for (*Scorpio* + *Pandinus* + *Heterometrus*), but independently derived in some species of *Opistophthalmus* (e.g. *O. capensis* and *O. holmi*).

Metasoma

77. *Metasomal segment V, dorsolateral carinae*: strong, continuous (0); weak to absent, discontinuous (1). [Merged BHL 66 and 67.] Weak to absent, discontinuous dorsolateral carinae are synapomorphic for *Opistophthalmus*, with reversals in some species (e.g. *O. capensis*), and an independent derivation in *S. maurus palmatus*.

78. *Metasomal segments II–IV, dorsosubmedian carinae, distal spiniform granules*: weak to absent (not noticeably larger than preceding granules) (0); moderate to strong (distinctly larger than preceding granules) (1). [Modified BHL 58: merged states 1 and 2 because these could not be objectively delimited.] As reconstructed under ACCTRAN, moderate to strong distal spiniform granules on the dorsosubmedian carinae of metasomal segments II–IV are synapomorphic for some derived species of *Opistophthalmus* (e.g. *O. carinatus* and *O. capensis*), but have also reversed to the plesiomorphic, weak to absent condition in other derived species (e.g. *O. holmi*).

79. *Metasomal segment V, dorsal surface, macrosculpture (♂)*: granular (0); smooth (1). [BHL 64] By comparison with the diplocentrid outgroup, absence of granulation on the dorsal surface of metasomal segment V in the ♂ is synapomorphic for the Scorpionidae (ACCTRAN), but reverses to the plesiomorphic, granular condition in *Scorpio*, several species of *Opistophthalmus* (e.g. *O. holmi*) and a few species of *Pandinus* (e.g. *P. cavimanus*).

80. *Metasomal segment V, dorsal surface, macrosculpture (♀)*: granular (0); smooth (1). [BHL 65] By comparison with the diplocentrid outgroup, absence of granulation on the dorsal surface of metasomal segment V in the ♀ is synapomorphic for the Scorpionidae (ACCTRAN), but reverses to the plesiomorphic granular condition in *Scorpio*, several species of *Opistophthalmus* (e.g. *O. holmi*) and a few species of *Pandinus* (e.g. *P. cavimanus*).

81. *Metasomal segments I–IV, ventrosubmedian carinae*: present and distinct on segments I–IV (0); absent or obsolete on segments I, I and II or I–IV (1). [Merged BHL 40, 45, 50, 51, 59 and modified, by merging states 1, 2 and 3.] Reduction or absence of the ventrosubmedian carinae on metasomal segments I, I and II or I–IV is synapomorphic for derived species of *Opistophthalmus* (including *O. carinatus*, *O. capensis* and *O. holmi*).

82. *Metasomal segments I–IV, ventrosubmedian and ventrolateral carinae*: more strongly developed on segments III and IV than on segments I and II (0); more strongly developed on segments I and II than on segments III and IV (1). [LP 96] Disproportionate development of the ventrosubmedian and ventrolateral carinae on segments I and II, relative to those on segments III and IV, evolved independently in

O. boehmi, *Scorpio* and *P. cavimanus*. This character state does not represent a synapomorphy of (*Opistophthalmus* + *Scorpio*) as hypothesised in a previous analysis (Prendini 2000*a*).

83. *Metasomal segment V, ventrolateral carinae, distally*: divergent (0); subparallel to convergent (1). [BHL 70] Subparallel to convergent ventrolateral carinae on metasomal segment V are synapomorphic for some derived species of *Opistophthalmus* (e.g. *O. capensis* and *O. holmi*).

84. *Metasomal segment V, ventrolateral carinae*: comprising rounded granules (0); comprising spiniform or denticulate granules (1). [BHL 69] The spiniform or denticulate condition of the granules comprising the ventrolateral carinae of metasomal segment V is synapomorphic for (*Pandinus* + *Heterometrus*). As reconstructed under ACCTRAN, the spiniform or denticulate condition is also synapomorphic for some derived species of *Opistophthalmus* (e.g. *O. carinatus* and *O. capensis*), but has reversed to the plesiomorphic, rounded condition in other derived species of the genus (e.g. *O. holmi*).

85. *Metasomal segment V, ventrolateral carinae, distal spiniform granules*: absent (not noticeably larger than preceding granules) (0); weakly developed (slightly larger than preceding granules) (1); strongly developed (distinctly larger than preceding granules) (2). [Incorporates HWC 113.] Weakly developed distal spiniform granules on the ventrolateral carinae of metasomal segment V are synapomorphic for (*Pandinus* + *Heterometrus*), with a reversal to the plesiomorphic absence of granules in *P. cavimanus*. Weakly developed distal spiniform granules are also synapomorphic for some derived species of *Opistophthalmus* (e.g. *O. capensis*), from which they transform into strongly spiniform granules (e.g. in *O. carinatus*) or reverse to plesiomorphic absence (e.g. in *O. holmi*).

86. *Metasomal segment V, ventromedian carina, distal portion*: unmodified (0); breaking up into numerous granules (1); inapplicable (–). [Part of LP 99.] A modification of the distal portion of the ventromedian carina of metasomal segment V evolved independently in *Scorpio* and *O. boehmi*. This character state does not represent a synapomorphy of (*Opistophthalmus* + *Scorpio*) as hypothesised in a previous analysis (Prendini 2000*a*). This character is inapplicable in the taxa without a ventromedian carina.

87. *Metasomal segment V, anal arch, anterior carina*: costate (0); serrate (1). The serrate anal arch of metasomal segment V also evolved independently in *Scorpio* and *O. boehmi*.

Telson

88. *Vesicle, shape*: globose (0); elongate (1). An elongate telson vesicle is synapomorphic for most South-East Asian *Heterometrus* (including *H. laoticus* and *H. spinifer*).

89. *Vesicle, surface macrosculpture*: longitudinal rows of granules on ventral and lateral surfaces (0); longitudinal rows of granules on all or part of ventral surface only (1); entirely smooth (2). [Merged BHL 73 and 74.] By comparison with the diplocentrid outgroup, the presence of longitudinal rows of granules on the ventral surface of the vesicle only is synapomorphic for the Scorpionidae, with a reversal to plesiomorphic presence on the ventral and lateral surfaces in some *Scorpio* (e.g. *S. maurus fuscus*). As reconstructed under ACCTRAN, complete absence of granulation on the vesicle is further derived in most *Opistophthalmus* (including *O. carinatus* and *O. capensis*), but also reverses to presence on the ventral surface only (e.g. in *O. holmi*).

Colour patterns

90. *Chelicerae, dorsal surfaces*: entirely pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace interocular surface) (0); bicoloured, dorsointernal half of manus much paler than dorsoexternal half and fingers (manus similar to or paler than carapace interocular surface) (1); entirely dark (manus darker than carapace interocular surface) (2). Bicoloured chelicerae are synapomorphic for the Scorpionidae, by comparison with the diplocentrid outgroup, but reversed to entirely pale chelicerae several times in the family (e.g. in *O. holmi* and *S. maurus palmatus*). Entirely dark chelicerae evolved from bicoloured chelicerae in some derived *Opistophthalmus* (e.g. in *O. capensis*).

91. *Carapace, interocular surface*: similar to or darker than lateral and posterior surfaces (0); noticeably paler than lateral and posterior surfaces (1). As reconstructed under ACCTRAN, a pale interocular surface is synapomorphic for some derived species of *Opistophthalmus* (e.g. *O. carinatus* and *O. capensis*), but reversed to the plesiomorphic 'similar to or darker than' condition in other derived species (e.g. *O. holmi*).

92. *Carapace, posterolateral and posteromedian surfaces*: as dark as or darker than tergites (0); as pale as tergites, if tergites not infuscated, or paler than tergites, if tergites infuscated (1). Pale posterolateral and posteromedian carapacial surfaces are synapomorphic for *Opistophthalmus* and independently derived in *Scorpio* (e.g. *S. maurus palmatus*).

93. *Pedipalps, infuscation*: none (0); infuscation of femur and patella only (1); infuscation of femur, patella and chela (2). As reconstructed under DELTRAN, the absence of pedipalp infuscation is plesiomorphic in the Scorpionidae although, of the species included in this analysis, only *O. boehmi*, *O. holmi* and *S. maurus palmatus* exhibit the condition. Infuscation of the femur and patella only is relatively derived and synapomorphic for (*Pandinus* + *Heterometrus*), although only observed in the East African exemplars of *Pandinus* (*P. cavimanus* and *P. viatoris*). Infuscation of femur, patella and chela is synapomorphic for *Heterometrus*, for the West African exemplars of *Pandinus* (*P. dictator* and *P. imperator*), and independently derived in *O. carinatus*, *O. capensis* and *S. maurus fuscus*.

94. *Tergites, overall coloration*: uniform (0); distal third noticeably paler (1). Distally pale tergites are synapomorphic for *Opistophthalmus* and independently derived in *Scorpio* (e.g. in *S. maurus palmatus*).

95. *Tergites, extent of infuscation (♀)*: little (less than two-thirds per tergite) to no infuscation (0); entirely or almost entirely (more than two-thirds) infuscated (1). By comparison with the diplocentrid outgroup, entirely or almost entirely infuscated tergites in the ♀ are synapomorphic for the Scorpionidae, but reversals to entirely pale tergites occurred several times in the family (e.g. in *O. holmi* and *S. maurus palmatus*).

96. *Metasoma, intercarinal surfaces (♀)*: dark (as dark as tergites, if pigmented) (0); metasomal segments, at least I and II or I–III, pale (as pale as tergites, if tergites have no pigmentation, or markedly paler than, if tergites pigmented) (1). As reconstructed under ACCTRAN, pale metasomal segments in the ♀ are synapomorphic for *Opistophthalmus*, with a reversal to the plesiomorphic dark condition in some species of the genus (e.g. *O. carinatus*). An independent derivation of pale metasomal segments occurs in *Scorpio* (e.g. in *S. maurus palmatus*).

97. *Ventrosubmedian and/or ventrolateral carinae, infuscation (which may be present even if the actual carinae are obsolete or absent)*: none (0); infuscation on metasomal segments III–V but not I and II, or on metasomal segments IV and V but not I–III (1); infuscation on metasomal segments I–V (2). As reconstructed under ACCTRAN, carinal infuscation on metasomal segments III–V or IV and V is synapomorphic for the Scorpionidae, although, of the species included in this analysis, only *O. boehmi* and *S. maurus palmatus* exhibit the condition. The occurrence in *S. maurus palmatus* represents a reversal from the relatively more derived condition of infuscation on metasomal segments I–V, which is synapomorphic for (*Scorpio* + *Pandinus* + *Heterometrus*). Infuscation on metasomal segments I–V is independently derived in some species of *Opistophthalmus* (e.g. *O. carinatus* and *O. capensis*) and reverses to the plesiomorphic absence of infuscation in other species (e.g. *O. holmi*).

98. *Sternites III–VII*: III–VI pale (no infuscation), although VII occasionally darkened (0); III–VII dark (1). Uniformly darkened

sternites are synapomorphic for (*Pandinus* + *Heterometrus*), with independent derivations in some *Opistophthalmus* (e.g. *O. capensis*).

99. *Legs, overall colour*: pale (although perhaps very lightly infuscated) (0); very dark or heavily infuscated (1). Darkened or heavily infuscated legs are synapomorphic for (*Pandinus* + *Heterometrus*), with reversals to the plesiomorphic pale condition in some *Heterometrus* (e.g. *H. fulvipes*).

Sternites–metasoma

100. *Sternite VII, longitudinal carinae*: four strongly developed carinae (paired ventrosubmedian and ventrolateral) (0); two weakly developed ventrolateral carinae (1); none (2). The presence of two weakly developed ventrolateral carinae on sternite VII is synapomorphic for (*Pandinus* + *Heterometrus*), with a reversal to the plesiomorphic condition of four strongly developed carinae in *P. cavimanus*. The complete absence of sternite carinae is further derived in most *Opistophthalmus* (including *O. carinatus*, *O. capensis* and *O. holmi*).

101. *Sternite VII, surface, and metasomal segment I, ventral surface, macrosculpture (♂)*: none (0); scattered granules (1); rounded tubercles (2). [Components of BHL 35, 42, 48, 55, and 61.] The occurrence of scattered granules on sternite VII and the ventral surface of metasomal segment I in the ♂ is synapomorphic for *Scorpio*, whereas the occurrence of rounded tubercles on these surfaces is independently derived in some *Opistophthalmus* (e.g. *O. capensis* and *O. holmi*).

102. *Metasomal segment II, ventral surface, macrosculpture (♂)*: none (0); scattered granules (1); rounded tubercles (2). [Components of BHL 35, 42, 48, 55, and 61.] The occurrence of scattered granules on the ventral surface of metasomal segment II in the ♂ is synapomorphic for *Scorpio*, and independently derived in some *Opistophthalmus* (e.g. *O. capensis*). The occurrence of rounded tubercles on this surface is further derived in other *Opistophthalmus* (e.g. *O. holmi*).

103. *Metasomal segment III, ventral surface, macrosculpture (♂)*: none (0); scattered granules (1); rounded tubercles (2). [Components of BHL 35, 42, 48, 55, and 61.] The occurrence of scattered granules on the ventral surface of metasomal segment III in the ♂ is synapomorphic for *Scorpio*, and independently derived in some *Opistophthalmus* (e.g. *O. carinatus* and *O. capensis*). The occurrence of rounded tubercles on this surface is further derived in other *Opistophthalmus* (e.g. *O. holmi*).

Behaviour

104. †*Burrows constructed in the open*: absent (0); present (1); unknown (?). By comparison with the diplocentrid outgroup, burrowing in open ground represents a potential synapomorphy for the Scorpionidae, but the character is uninformative in the present analysis. This character was scored unknown in *H. laoticus*, *H. spinifer*, *P. cavimanus*, *P. dictator* and *P. imperator*, for which no data were available.

105. *Burrows constructed under stones*: present (0); absent (1); unknown (?). Burrowing under stones is plesiomorphic in the Scorpionidae, by comparison with the diplocentrid outgroup. Burrowing exclusively in open ground (or the 'absence' of burrowing under stones) has evolved on several occasions in *Opistophthalmus* and *Scorpio*, the occurrence of this state in *O. boehmi*, *O. holmi* and *S. maurus palmatus* representing three independent origins. This character was scored unknown in *H. fulvipes*, *H. laoticus*, *H. spinifer*, *H. swammerdami*, *P. cavimanus* and *P. viatoris*, for which no data were available.

106. *Mesosomal percussion (♂)*: absent (0); present (1). [LP 115] Mesosomal percussion in the ♂ is synapomorphic for *Scorpio*.