



## Biodiversity/Biodiversité

## The genus *Hormiops* Fage, 1933 (Hormuridae, Scorpiones), a palaeoendemic of the South China Sea: Systematics and biogeography



### *Le genre Hormiops Fage, 1933 (Hormuridae, Scorpiones), un paléoendémique de la mer de Chine méridionale : systématique et biogéographie*

Lionel Monod

Département des arthropodes et d'entomologie I, Muséum d'histoire naturelle, route de Malagnou, 1, 1208 Genève, Switzerland

## ARTICLE INFO

## Article history:

Received 30 May 2014

Accepted after revision 28 July 2014

Available online 5 September 2014

## Keywords:

Scorpion  
Hormuridae  
*Hormiops*  
Vietnam  
Malaysia  
Lithophilous  
Palaeoendemic

## Mots clés :

Scorpion  
Hormuridae  
*Hormiops*  
Vietnam  
Malaysia  
Lithophile  
Paléoendémique

## ABSTRACT

The monotypic genus *Hormiops* Fage, 1933 is so far only known from two groups of granitic islands off the coasts of Peninsular Malaysia and Vietnam. Examination of newly collected material from both archipelagos and of the type series of *Hormiops davidovi* Fage, 1933 reveals previously disregarded morphological differences sufficient to assign the Malaysian specimens to a distinct species, described here as *Hormiops infulcra* sp. nov. An updated diagnosis of the genus, as well as a dichotomic key enabling the determination of *Hormiops* from its close relatives, *Hormurus* Thorell, 1876 and *Liocheles* Sundevall, 1833 are also provided. The phylogenetic position, distribution pattern, and ecology of these insular scorpions suggest that they are palaeoendemics, remnants of a previously more widely distributed lineage. A biogeographical model is proposed for the genus based on these observations and on a synthesis of palaeogeographical and palaeoenvironmental data currently available for Sundaland.

© 2014 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

## R É S U M É

Le genre monotypique *Hormiops* Fage, 1933 est actuellement uniquement répertorié dans deux groupes d'îles granitiques au large des côtes malaisiennes et vietnamiennes. L'étude de spécimens récemment récoltés dans ces deux archipels ainsi que de la série typique de *Hormiops davidovi* Fage, 1933 a permis de mettre en évidence de nouvelles différences morphologiques suffisantes pour placer les spécimens malais dans une espèce distincte, décrite ici comme *Hormiops infulcra* sp. nov. Une diagnose révisée du genre, ainsi qu'une clé de détermination pour *Hormiops* et ses proches parents, *Hormurus* Thorell, 1876 et *Liocheles* Sundevall, 1833 sont également fournis. La position phylogénétique, le modèle de distribution et l'écologie de ces scorpions insulaires suggèrent qu'il s'agit de paléoendé-

E-mail address: [lionel.monod@ville-ge.ch](mailto:lionel.monod@ville-ge.ch).<http://dx.doi.org/10.1016/j.crv.2014.07.009>

1631-0691/© 2014 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

miques, vestiges d'une lignée précédemment plus répandue. Un modèle biogéographique est proposé pour le genre sur la base de ces observations et d'une synthèse des données paléogéographiques et paléoenvironnementales actuellement disponibles pour le Sundaland.

© 2014 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

## 1. Introduction

The hormurid genus *Hormiops* Fage, 1933 was described from three specimens collected by the Russian zoologist Constantine Dawydoff on the Vietnamese Côn Sơn Island, formerly known as Poulo Condore and part of the Côn Đảo Archipelago. The validity of this monotypic genus has been controversial since 1989. Lourenço [1] considered that *Hormiops* should be placed in the synonymy of *Liocheles* Sundevall, 1833. Fet [2] subsequently suggested that *Hormiops davidovi* Fage, 1933 (Fig. 1A, C) was a junior synonym of *Liocheles australasiae* (Fabricius, 1775), arguing that the former was found within the distribution range of the latter. Lourenço and Monod [3] reinstated the genus, but their decision was based solely on the examination of the type material and not on a phylogenetic analysis. Prendini [4] deemed the diagnostic characters insufficient for a generic distinction, and synonymized *Hormiops* with *Liocheles* again, but he did not provide phylogenetic evidence to support the taxonomic change. However, contrary to Fet [2], Prendini [4]

recognized *Liocheles davidovi* (Fage, 1933) [= *H. davidovi* Fage, 1933] as a valid species. *Hormiops* was finally reinstated as a valid genus by Monod and Prendini [5] based on a proper phylogenetic framework.

*Hormiops* is so far only known from two groups of granitic islands of the South China Sea, i.e. the Côn Đảo Archipelago near the southern tip of Vietnam and the Seribuat Archipelago off the southeastern coast of Peninsular Malaysia. Specimens from Pulau Tioman, the largest island of the Seribuat Archipelago [6], were first mentioned and identified as *H. davidovi* by Kovařík [7]. However, about 700 km of open sea separate Tioman from Côn Sơn, suggesting that the specimens found on the Malaysian island most likely belong to a distinct species [8]. Field surveys were conducted in both archipelagos in order to collect fresh material to clarify the status of the Tioman populations. Examination of the scorpions collected during these expeditions and comparison with *H. davidovi* type material confirmed that the Tioman specimens belong to an unknown species, described here as *Hormiops infulcra* sp. nov. (Fig. 1B, D). The fresh specimens also enable us to

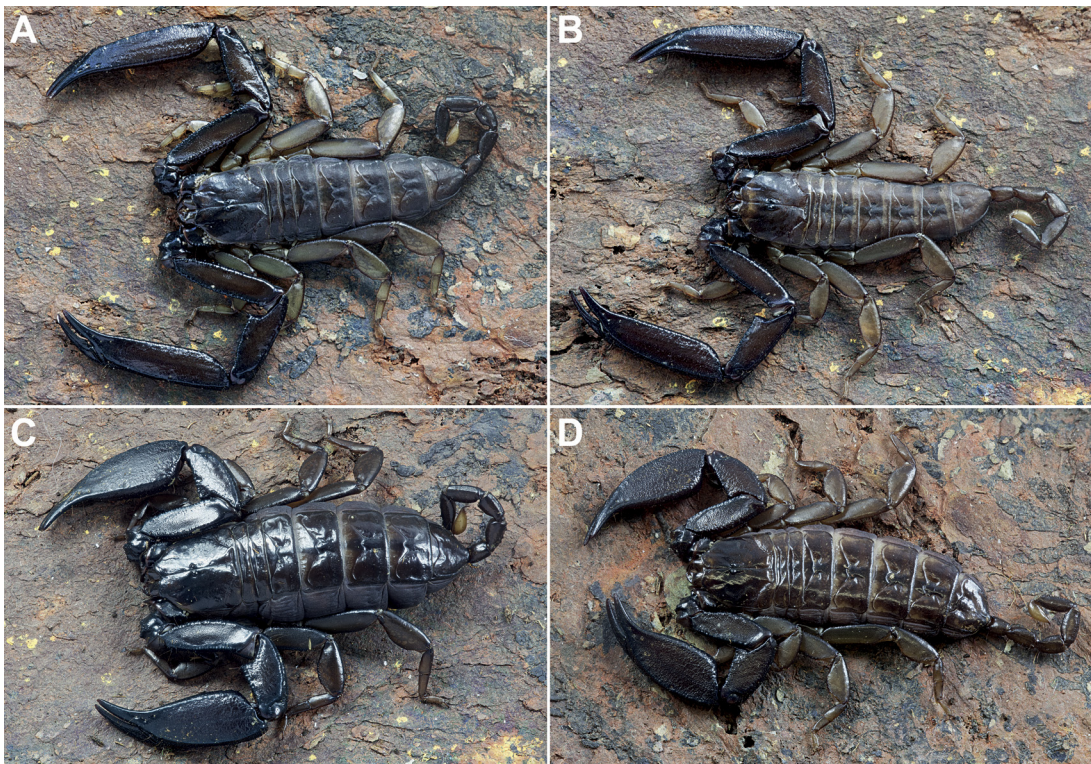


Fig. 1. (Colour online.) Habitus of the hormurid genus *Hormiops* Fage, 1933. *Hormiops davidovi* Fage, 1933, male (A) and female (C). *Hormiops infulcra* sp. nov., male (B) and female (D).

thoroughly examine characters previously unknown or inadequately studied, such as cuticle ornamentation, hemispermatophores, and book lungs. Based on these new data and on observations made in the field, a revised diagnosis of the genus, a determination key to the Australasian hormurid genera, as well as a description of the ecomorphotype and habitat of these scorpions, both previously unknown, are provided. Furthermore, a biogeographic hypothesis is proposed to explain the disjunct distribution of the genus in Southeast Asia, based on the current phylogeny of the Indo-Pacific hormurids [5] and on a synthesis of Sundaland geomorphological history.

## 2. Material and methods

### 2.1. Fieldwork

Most specimens examined were collected during field surveys in Vietnam and Malaysia. Scorpions were collected during the day by inspecting rock crevices and exfoliations, and at night with ultraviolet (UV) light [9] using a portable Maglite lamp equipped with a UV led retrofit (Xenopus Electronix, Austin, TX, USA).

### 2.2. Georeferencing

Exact geographical coordinates of collecting localities were recorded using a portable GPS device (Garmin E-trek Summit). Only coarse data, rounded to the nearest 10 seconds, are provided in the present publication following the recommendations of Chapman and Grafton [10]. Geographical coordinates for records without GPS data were traced by reference to gazetteers and the Geonet Names server (<http://earth-info.nga.mil/gns/html/index.html>) and are given between brackets.

### 2.3. Abbreviations

Collections containing material examined in the present study are abbreviated as follows: MHNG, Muséum d'histoire naturelle (Geneva, Switzerland); MMUM, Manchester Museum, University of Manchester (Manchester, U.K.); MNHN, Muséum national d'histoire naturelle (Paris, France); RMBR, Raffles Museum of Biodiversity Research (Singapore).

### 2.4. Examination and dissection

Specimens were examined with a Zeiss Stemi SV8 stereomicroscope. Hemispermatophores were dissected from adult male specimens using microsurgical scissors and forceps immediately after specimens were euthanized. Paraxial organ tissues were then removed manually with forceps. Dissecting the specimens as early as possible ensure that paraxial organ tissues have not stiffened yet and can be removed more easily without damaging the hemispermatophores. This is particularly recommended for small, weakly sclerotized hemispermatophores like those of *Hormiops*.

### 2.5. Morphological terminology

Morphological terminology follows Stahnke [11] for pedipalp segmentation, Vachon [12] for trichobothrial patterns, Couzijn [13] for leg segmentation, Lamoral [14] and Monod and Volschenk [15] for hemispermatophore, and Prendini [4] for carapace sulci and sutures, and pedipalp and metasomal carinae.

### 2.6. Photographs and illustrations

High-resolution images of diagnostic characters were taken under long-wave UV and visible light with a custom-built stacking system at the MHNG. Zerene Stacker (Zerene Systems, Richland, WA, USA) was used to fuse images taken at different focal planes into a single image with a greater depth of field. Line drawings of hemispermatophores were produced using a camera lucida mounted on the stereomicroscope. Pencil sketches were subsequently inked and scanned for further processing and editing. Illustrations and photographs were edited (background removal and contrast adjustment) in Adobe Photoshop CS5 and plates prepared with Adobe Illustrator CS5 (both from Adobe systems, San Jose, CA, USA).

### 2.7. Phylogenetic analysis

*Hormiops infulcra* sp. nov. was added to the dataset of Monod and Prendini [5]. Based on new observations of the metasomal segment I, two characters of the previous matrix (98, 99) were merged into one (101), and three new characters (93–95) were coded for each taxa. The matrix was compiled with Mesquite version 2.75 [16] and is provided in the supplementary material, as well as the list of characters and character states.

One hundred and nine of the 141 discrete characters were coded into binary states and 32 were coded into multistates. Evolutionary transformation sequences could not be inferred for eight multistate characters (7, 48, 59, 76, 88, 128, 134) which were treated as nonadditive (unordered) [17]. The remaining 26 multistate characters (4, 9, 10, 12, 23, 32, 33, 34, 41, 43, 46, 51, 52, 63, 67, 71, 81, 82, 101, 106, 107, 117, 123, 126, 127, 132), discretized continuous variation reflecting a linear evolutionary transition, were treated as additive (ordered) [18]. Characters were not weighted *a priori*.

Twenty-five uninformative characters (3, 6, 12, 19, 22, 42, 47, 50, 53, 56, 59, 61, 62, 65, 68, 72, 82, 85, 96, 97, 109, 112, 115, 119, 141), detected with the “mop uninformative chars” function in Winclada version 1.00.08 [19], were excluded from the analysis. The analysis and tree statistics are thus based on 121 phylogenetically informative characters.

Parsimony analysis was conducted with new technology heuristic search strategies, i.e. sectorial searches, tree-drifting and tree-fusing [20], implemented in TNT version 1.1 [21,22]. An equal weighting (EW) analysis was initially performed with 100 random taxon addition replicates as starting points. Each replication was initially auto-constrained with Wagner and previously inferred trees. Constrained and random sectorial searches with 200



parsimony ratchet [23] iterations, 50 iterations of tree drifting and 10 rounds of tree fusing were performed at each replication. The maximum number of trees held in memory was initially set to 10,000. The cladogram presented here was generated as a metafile from TNT and subsequently edited in Illustrator CS3 (Adobe Systems, San Jose, CA, USA).

A sensitivity analysis (sensu Wheeler [24]) was undertaken in order to assess the robustness of clade support and the stability of tree topologies under different weighting regimes. Implied weighting (IW) analyses [25,26] with concavity ( $K$ ) values ranging from 1 to 10 were performed on the dataset. A preferred hypothesis was selected from among the equally parsimonious alternatives, according to three criteria: maximum fit, minimum length, maximum congruence with the topological result of the sensitivity analysis. The tree was collapsed under “rule 1” [27,28].

The relative degree of support for each node was assessed for the phylogeny selected with symmetric resampling (SR) frequencies [29]. 10,000 pseudoreplicates were used to calculate the frequencies with the probability to increase and decrease character weight set to the default value ( $P=0.33$ ). Suboptimal trees were generated from 10 random addition sequences submitted to tree-bisection-reconnection (TBR) branch-swapping and up to 10 trees were kept per replication. Frequencies were reported on the preferred tree as GC (‘Group present/Contradicted’) scores.

## 2.8. Reproductive biology

Several males and females of both species were kept in captivity in order to conduct observations on their sexual behaviour and gestation periods. Temperatures were maintained between 25 and 30 °C without seasonal changes. Each specimen was housed individually in plastic containers and fed 2–4 crickets every two weeks. Several females, gravid when collected, gave birth in the laboratory. Mating experiments were performed by placing female/male pairs in a larger plastic container. The bottom of this “arena” was covered with a thin sheet of cork bark, moistened on one side in order to create a humidity gradient across the enclosure. Inseminated females were maintained under the same laboratory conditions until they gave birth.

## 3. Systematics

Family: **HORMURIDAE** Laurie, 1896

### Determination key to Australasian hormurid genera

1. Carapace with three pairs of lateral ocelli and distinct anterior furcated suture and sulci. Metasomal segment I not flattened dorso-ventrally (as high as wide, and about the same width and height as following segments); ventrolateral and ventro-submedian carinae parallel to the longitudinal axis of the segment; ventro-submedian carinae not fused distally, distinct along total length of segment (Fig. 2C–E). Telson equal or slightly longer than metasomal segment V .....2.

Carapace with two pairs of lateral ocelli and with anterior furcated suture and sulci vestigial or absent. Metasomal segment I flattened dorso-ventrally (wider than high, wider than following segments, lower than following segments); ventrolateral and ventro-submedian carinae converging to the same point near the posterior margin of the segment; ventro-submedian carinae distinct in anterior half, fused into a single carina in posterior half (Fig. 2A–B). Telson shorter than metasomal segment V.....*Hormiops*.

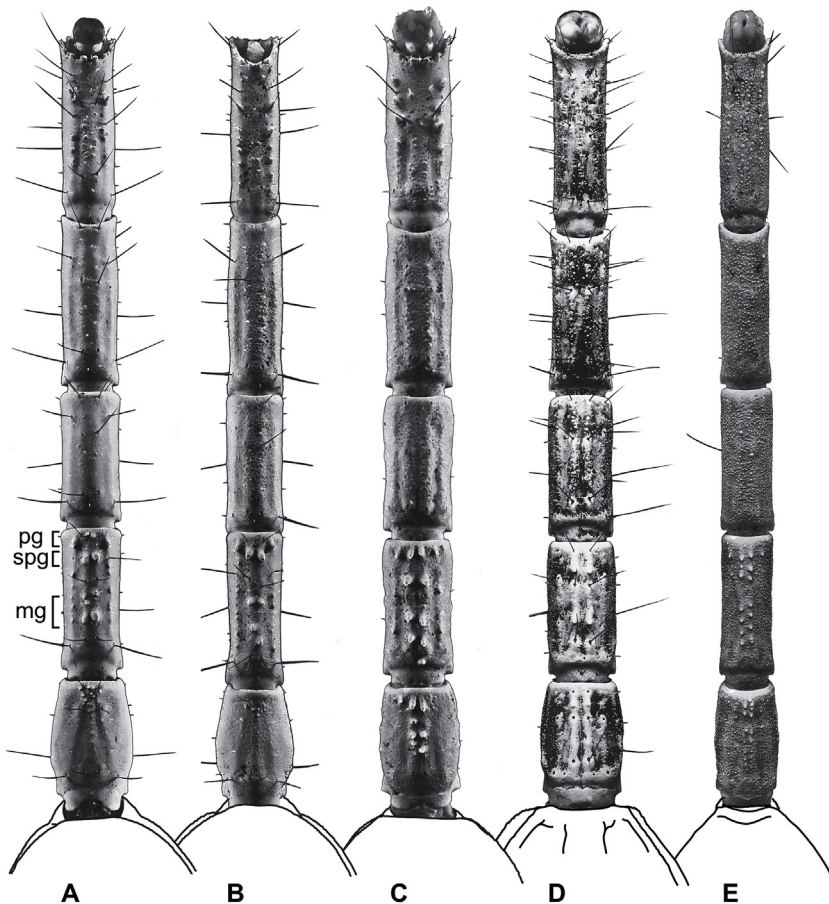
2. Retrolateral surface of chela manus: *Esb* proximal, aligned with *Eb* series.....*Liocheles*

Retrolateral surface of chela manus: *Esb* distal to *Eb* series, at least midway between *Eb* series and *Est*.....*Hormurus*

Genus: ***Hormiops*** Fage, 1933

**Remark:** A revised and updated diagnosis of the genus is warranted by the discovery of the new species *H. infulcra*, which does not share several characters of *H. davidovi* that were given in the previous diagnosis of the genus [5]. Moreover, the types series of *Hormiops davidovi* suffered from a prolonged stay in substandard preservative. The specimens have lost their pigmentation and fluorescence, preventing a thorough examination of cuticular macro-sculptures. The availability of fresh material collected in the course of this study allowed an accurate study and imaging of these structures by means of UV lighting and led to the discovery of important additional diagnostic characters for the carination of the metasomal segment I.

**Diagnosis** (modified and completed from Monod and Prendini [5]): *Hormiops* differs from *Hormurus* and *Liocheles* in the following combination of characters. The carapace is flat in *Hormiops*, whereas the median ocular tubercle is at least slightly raised in *Hormurus* and *Liocheles*. The anterior furcated suture and sulci are vestigial or absent in *Hormiops*, but present in *Hormurus* and *Liocheles*. Two pairs of lateral ocelli are present in *Hormiops*, whereas three pairs are present in *Liocheles* and *Hormurus* species except the troglobite, *H. polisorum* (Volschenk, Locket & Harvey, 2001). Lateral transverse sulci are absent or at most very shallow on the mesosomal tergites in *Hormiops*, but present in *Hormurus* and *Liocheles*. The metasomal segment I is flattened dorso-ventrally (as wide as high, and wider than following segments) in *Hormiops* (Fig. 2A–B), whereas it is as high as wide, and about the same width as following segments in *Hormurus* and *Liocheles* (Fig. 2C–E). Metasomal segments II–V are laterally compressed (higher than wide) in *Hormiops*, whereas they are rounded in *Hormurus* and *Liocheles*. The ventrolateral and ventro-submedian carinae of metasomal segment I converge to the same point near the posterior margin of the segment in *Hormiops* (Fig. 2A–B), whereas they are parallel to the longitudinal axis of the segment in *Hormurus* and *Liocheles* (Fig. 2C–E). The ventro-submedian carinae of metasomal segment I are distinct in anterior half, fusing into a single carina in posterior half in *Hormiops* (Fig. 2A–B), whereas they are not fused distally and distinct along the total length of the segment in *Hormurus* and *Liocheles*. The telson is shorter than metasomal segment V in *Hormiops*, whereas it is equal to or slightly longer in *Hormurus* and *Liocheles*.



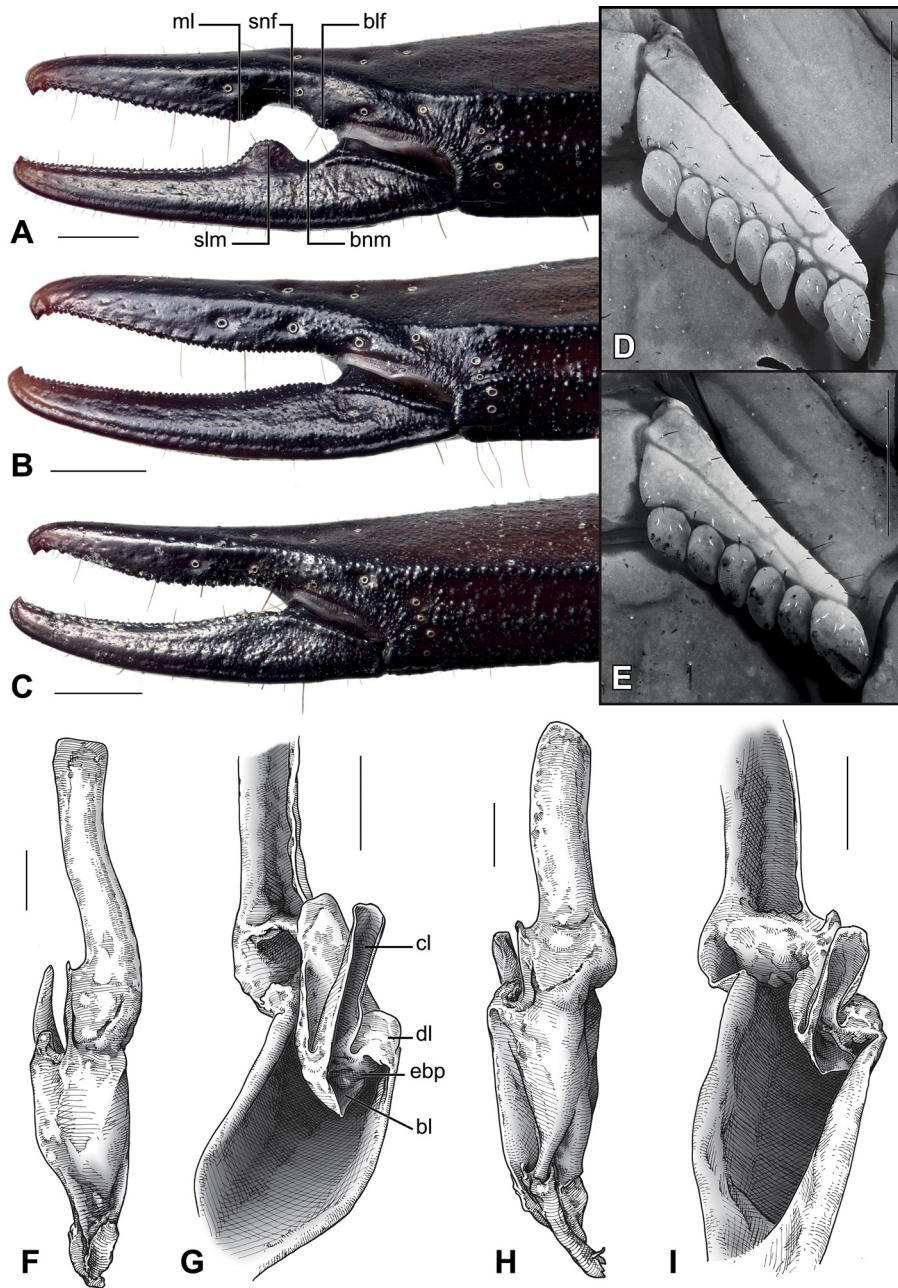
**Fig. 2.** Ventral aspect of metasoma in the genera *Hormiops* Fage, 1933, *Hormurus* Thorell, 1876 and *Liocheles* Fabricius, 1889. A. *Hormiops davidovi* Fage, 1933. B. *Hormiops infulcra* sp. nov. C. *Liocheles* sp., W Java, Indonesia. D. *Hormurus ischnoryctes* Monod & Prendini, 2013. E. *Hormurus longimanus* (Lockett, 1995). Abbreviations: mg (medial granules, ventro-submedian carinae), pg (posterior granules, lateral and ventro-submedian carinae), spg (subposterior granules, ventro-submedian carinae).

*Hormiops* differs further from *Hormurus* in the following characters. The proximal part of the finger is smooth and trichobothria *db*, *dsb* and *dst* are not surrounded by granules delimiting smooth depressions in *Hormiops*, whereas the surface of the finger is granular with *db*, *dsb* and *dst* located in distinct, smooth depressions in *Hormurus*. Pedipalp chela trichobothrium *Esb* is proximal and aligned with the *Eb* series in *Hormiops*, whereas *Esb* is distal to the *Eb* series, usually situated midway between the *Eb* series and *Est* or close, and sometimes slightly distal to *Est* in *Hormurus*. Posterior spiniform granules on the ventrolateral carinae of metasomal segment II, present in *Hormiops* (Fig. 2A–B), are absent or vestigial in *Hormurus* (Fig. 2D–E).

*Hormiops* differs further from *Liocheles* in the following characters. Pronounced posterior spiniform granules, absent or vestigial on the ventrosubmedian carinae of metasomal segments I and II in *Hormiops* (Fig. 2A–B), are present in *Liocheles* (Fig. 2C). The apex of the capsular lamella of the hemispermatophore is aligned with or proximal to the base of the laminar hook in *Hormiops* (Fig. 3F–I), whereas it is aligned with or slightly distal to the apex of the hook in *Liocheles*.

**Reproductive biology:** Under laboratory conditions, the gestation period in both species varies between 7 and 9.5 months. Three females of *H. davidovi* gave birth seven, eight and nine months after the copulation respectively and two females of *H. infulcra* sp. nov. after 8.5 and 9.5 months. The size of broods varies between seven and 30 juveniles. Eleven *H. davidovi* females initially collected gave birth to 7, 9 (2×), 12 (2×), 13 (2×), 14, 20, 23, and 30 juveniles, respectively. Broods of the eleven initially gravid *H. infulcra* sp. nov. females comprised 8, 9, 10 (3×), 15, 17, 23, 24, and 27 juveniles (2×), respectively. The three *H. davidovi* females fecundated in the laboratory gave birth to 12, 16 and 19 juveniles respectively, and the two *H. infulcra* sp. nov. to 15 and 18.

The sex ratio of the broods is not provided because the first instars are two small to be sexed with accuracy without causing stress and thus significantly increasing the relatively high mortality rate in the first stages of development. Moreover, broods were kept communally in order to increase survival rate and, although juveniles of both species are relatively tolerant toward individuals of the same brood, occasional cases of cannibalism do occur.



**Fig. 3.** (Colour online.) Diagnostic characters for males of *Hormiops davidovi* Fage, 1933 (A, B, D, F, G) and *Hormiops infulcra* sp. nov. (C, E, H, I). Pedipalp chela, retrolateral aspect, illustrating dentate margin of chela fingers (A, B, C). Left pectine (D, E). Left hemispermatophore, dorsal aspect (F, H) and detail of capsular region, ventral aspect (G, I). (A, D, F, G) MHNG, VMI-12/04. (B) MHNG, VMI-12/07. (C, E, H, I) Holotype (MHNG, VMI-12/14). Abbreviations: bl (basal lobe), blf (basal lobe, fixed finger), bnm (basal notch, movable finger), cl (capsular lamella), dl (distal lobe), ebp (ental basal process), ml (median lobe), slm (suprabasal lobe, movable finger), snf (suprabasal notch, fixed finger). Scale, 1 mm (A–E), 0.5 mm (F–G).

Therefore, once the specimens were large enough to be sexed (third–fourth instars), it was not possible to determine the initial male/female ratio.

**Remark:** A manuscript including complete descriptions and imaging of both species has been submitted for publication in a taxonomic journal and should be available in the coming months.

#### *Hormiops davidovi* Fage, 1933

*H. davidovi* Fage [30]: 32–33, fig. 1, 2, pl. I, figs a–c; Fage [31]: 181; Kästner [32]: 234, fig. 215; Takashima [33]: 94, 95; Fage [34]: 71; Vachon [12]: fig. 80; Kovařík [35]: 132; Lourenço and Monod [3]: 343, 344, figs 1–4.

*Hormiops davydovi* [misspelling]: Monod and Prendini [5]: Fig. 1A; 15–16, 24–25, 34.



*Liocheles australasiae*: Fet [2]: 395.

*L. davidovi*: Prendini [4]: 72; Monod and Volschenk [15]: 686.

**Syntypes:** Vietnam, Poulo Condore [= Côn Sơn Island, N08°42'00" E106°36'00"], S off the coast of Vietnam; II.1930/IV.1931; in forest, under stones, M. C. Dawydoff, 1 ♂, 1 ♀, 1 juv. (MNHN-RS 0562).

**Other material:** Vietnam, Poulo Condore Island [= Côn Sơn Island, N08°42'00" E106°36'00"], M. Germain, 1 ♀, 11 juv. (MNHN-RS 0499). Côn Đảo NP, Côn Sơn Island, track to Ong Dung Beach, 8.I.2012, rainforest, in rock crevices (granitic boulders), L. Monod, 1 ♂, 3 ♀♀ (MHNG VMI-12/01). Côn Đảo N.P., Côn Sơn Island, track to Soy Ray plantation, N08°41' E106°35', 50–180 m, 9.I.2012, rainforest, in rock crevices, L. Monod, 4 ♂♂, 4 ♀♀, 20 juv. (MHNG VM-12/02). Côn Đảo N.P., Côn Sơn Island, track to Dat Tham Beach, N08°42' E106°35', 150 m, 10.I.2012, rainforest, in rock crevices, L. Monod, 2 ♂♂, 4 ♀♀ (MHNG VMI-12/04). Côn Đảo N.P., Côn Sơn Island, track to Dam Tre Bay, N08°44' E106°39', 15–70 m, 11.I.2012, rainforest, in rock crevices, L. Monod, 1 ♂, 5 ♀♀, 2 juv. (MHNG VIM-12/07). Côn Đảo N.P., Ba Island, N08°38' E106°33', 60 m, 12.I.2012, rainforest, in rock crevices, L. Monod, 1 ♀ (MHNG VMI-12/10).

**Distribution and ecology:** *H. davidovi* is only known from, and probably endemic to, the Côn Đảo Archipelago, a group of granitic islands near the southern tip of Vietnam. Specimens were collected from narrow rock crevices of granitic outcrops in primary evergreen forests. The habitat and habitus are consistent with the lithophilous ecomorphotype [36].

**Conservation status:** the known populations of *H. davidovi* are located on several protected islands that are part of the Côn Đảo National Park. Although this species is currently not threatened by habitat destruction, the land area of the islands on which it was found is small (less than 80 km<sup>2</sup>). Because it is thus vulnerable to potential threats from tourism and loss of habitat in the future, it is recommended that *H. davidovi* be placed in the IUCN Red List of near threatened species [37].

***Hormiops infulcra* sp. nov.**

*H. davidovi* [misidentification]: Kovařík [7]: 57–58, figs 1–7.

**Holotype:** W MALAYSIA, PAHANG, Pulau Tioman, track from Genting to Paya, N02°46' E104°07', 70 m, 25.I.2012, rainforest, in rock crevices, L. Monod, ♂ (MHNG VMI-12/14).

**Paratypes:** Same data as holotype, 3 ♂♂, 2 ♀♀, 5 juv. (MHNG VMI-12/14). Pulau Tioman, foothills of Gunung Kajang, N02°47' E104°07', 60 m, 1–2.X.2001, rainforest, in rock crevices, L. Monod, 10 ♂♂, 13 ♀♀, 46 juv. (MHNG). Pulau Tioman, track near Mukut, N02°44' E104°07', 115 m, 23.I.2012, rainforest, in rock crevices, L. Monod, 4 ♂♂, 7 ♀♀, 14 juv. (MHNG VMI-12/12). Pulau Tioman, track near Nipah, N02°45' E104°07', 25 m, 24.I.2012, rainforest, in rock crevices, L. Monod, 4 ♂♂, 2 ♀♀, 2 juv. (MHNG VMI-12/13). Pulau Tioman, track from Japamala Resort to Lanting, N02°44' E104°07', 65 m, 27.I.2012, rainforest, in rock crevices, L. Monod, 2 ♂♂, 1 ♀♀ (MHNG VMI-12/15).

**Additional material:** Pulau Tulai [N02°54'44" E104°06'26"], 23.VIII.2003, P. K. L. Ng et al., 1 ♀, 4 juv. (RMBR ZRC.ARA.456), 1 juv. (RMBR ZRC.ARA.457).

**Etymology:** the name *infulcra* is a constructed from the Latin words “in” [not, without] and the nominative plural of “fulcrum”. The epithet is an invariable noun in apposition and refers to the absence of fulcra in the pectines.

**Diagnosis:** *H. infulcra* sp. nov. differs from *H. davidovi* by the following combination of characters. *H. infulcra* sp. nov. is distinctly smaller and slightly lighter in colour than *H. davidovi*. The prosomal carapace of males is slightly less densely granular in *H. infulcra* sp. nov. than in *H. davidovi*. The exteroventral carinae of the pedipalp femur is granular in *H. infulcra* sp. nov., whereas it bears coarse spiniform granules in *H. davidovi*. The dorsoexternal carina of the pedipalp patella in *H. infulcra* sp. nov. is costate-granular and more distinct than the faint costate ridge observed in *H. davidovi*. The digital carina of the pedipalp chela is granular in *H. infulcra* sp. nov., whereas it is costate in *H. davidovi*. In males of *H. infulcra* sp. nov. the dentate margins of the fixed and movable chela fingers are linear (Fig. 3C), whereas most males of *H. davidovi* possess a well-developed suprabasal lobe on the movable finger and a corresponding suprabasal notch on the fixed finger (Fig. 3A). The telotarsi IV has four proventral macrosetae in *H. infulcra* sp. nov., whereas they bear five in *H. davidovi*. The average number of pectinal teeth is six for males and five for females in *H. infulcra* sp. nov., whereas males and females of *H. davidovi* usually have seven and six pectinal teeth, respectively. The pectinal fulcrae are absent in *H. infulcra* sp. nov. (Fig. 3E), but present in *H. davidovi* (Fig. 3D). The tergites of males are less granular medially in *H. infulcra* sp. nov. than in *H. davidovi*. Moreover, in *H. infulcra* sp. nov. males, the posterior margins of tergites I–V are smooth medially and the median ridges are sometimes smooth as well, whereas tergites are completely granular in *H. davidovi* males. The metasoma is finely and sparsely granular in *H. infulcra* sp. nov. whereas it is smooth or nearly so in *H. davidovi*. The ventrosubmedian carinae of metasomal segment II have no granules posteriorly in *H. infulcra* sp. nov. (Fig. 2B), whereas they bear two small posterior spiniform granules in some specimens of *H. davidovi* (Fig. 2A). The hemispermatophore distal lamina is straight and only slightly longer than the basal part in *H. infulcra* sp. nov. (Fig. 3H), whereas it is slightly curved and longer than the basal part in *H. davidovi* (Fig. 3F).

**Distribution and ecology:** *H. infulcra* sp. nov. is only known from two islands of the Seribu Archipelago (Rompin District, Pahang State, Peninsular Malaysia) and is probably endemic to this group of granitic islands. On Pulau Tioman, scorpions were collected in primary rainforests, for the most part in narrow crevices of granitic outcrops. Few specimens were found under the bark and in holes of fallen logs or standing trees, but these were most likely accidental occurrences as previously noted for the Australian *Hormurus longimanus* (Lockett, 1995) [38]. *H. infulcra* sp. nov. is common on Pulau Tioman. Crevices inspected were usually inhabited by several specimens, suggesting high population densities. Although these scorpions are primarily stenotopic rock dwellers, the limited quantity of crevices in granite probably constrains specimens to seek alternative refuges when populations grow too large. The habitat and habitus of this species are

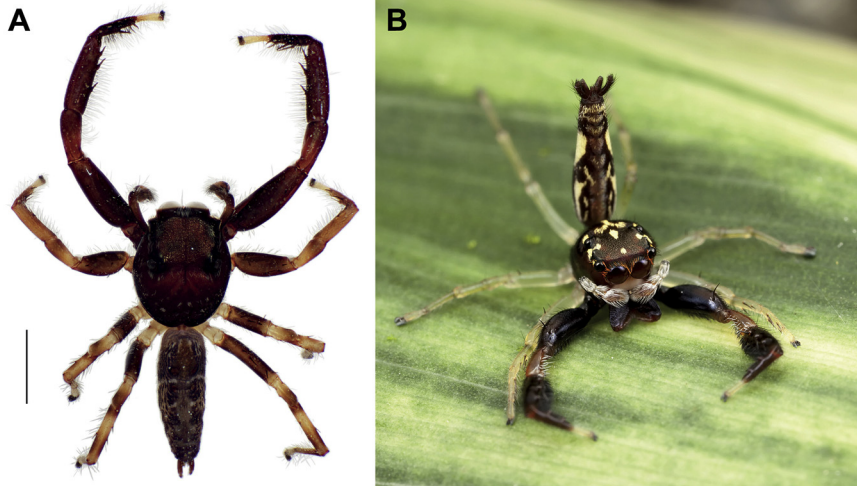


Fig. 4. (Colour online.) A. *Bavia sexpunctata* (Doleshall, 1859), male, Pulau Tioman, Seribuat Archipelago, Pahang, Malaysia (MMUM, G7549.1). B. Unidentified salticid spider (male) from Sungai Congkak Recreational Forest (Hulu Langat, Selangor, Malaysia) in defensive position. Scale, 2.5 mm.

consistent with the lithophilous ecomorphotype [36]. *H. infulcra* sp. nov. was found in syntopy (*sensu* Rivas [39]) with *Liocheles australasiae*.

**Conservation status:** Most known populations of *H. infulcra* sp. nov. are situated in protected rainforests of the Pulau Tioman Wildlife Reserve. Although this species is currently not threatened by habitat destruction, the land area of the islands on which it is found is small (133.6 km<sup>2</sup>). *H. infulcra* sp. nov. is thus deemed vulnerable to potential threats in the future, especially from tourism and loss of habitat, and it is recommended that it be placed in the IUCN Red List of near-threatened species [37].

**Remarks:** The salticid *Bavia sexpunctata* (Doleshall, 1859) (Fig. 4A) was collected together with the scorpions on Pulau Tioman. The spider was moving in a way similar to that of a scorpion, not using its first pair of legs to walk, but rather holding them up in the air like a scorpion holds its pedipalps. Although about half of the size of an adult *H. infulcra* sp. nov., the habitus of the spider is reminiscent of that of an adult *H. infulcra* sp. nov. male with the typical elongated pedipalps of the genus. Several Asian salticid genera, i.e. *Bavia* Simon, 1877, *Viciria* Thorell, 1877, *Stagetillus* Simon, 1885 and *Thianitara* Simon, 1903, possess a comparable habitus and when threatened, some species have been observed to adopt a defence posture resembling that of a scorpion with pedipalps outstretched and metasoma raised (Fig. 4B). It is possible that these strange salticid spiders mimic scorpions; however, further studies are necessary to confirm this.

#### 4. Biogeography of *Hormiops*

A recent biogeographic analysis of Indo-Pacific hormurid scorpions [5] suggests that hormurids colonized Laurasia from Gondwanaland via the Apulian microplate about 130 Ma ago, establishing a lineage in the northern hemisphere distinct from the African stock. These Laurasian scorpions, ancestors of the extant Australasian genera *Hormiops*, *Hormurus* and *Liocheles*, subsequently reached equatorial latitudes and were probably well

established in Southeast-Asian monsoon and perhumid ecosystems by the Mid–Late Cretaceous.

The monophyly of *Hormiops* and its sister relationship to *Liocheles* are unambiguous (Fig. 5), suggesting that this is a rather ancient lineage. *Hormiops* has, so far, never been recorded from continental Southeast Asia, it is only known from two archipelagos in the South China Sea, whereas *Liocheles* is widespread on the mainland. Field work and examination of museum collections indicates that this distribution is most likely not a sample bias. However, it is not clear whether the known extant populations of *Hormiops* are the remnants of a former, more widespread distribution, or whether this disjunction is the result of *in situ* speciation on one of the archipelagos followed by dispersal to the second across the South China Sea.

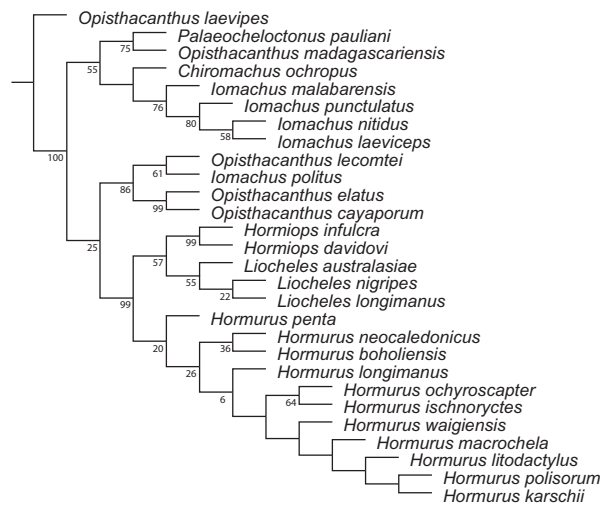


Fig. 5. Most parsimonious tree (MPT) obtained by cladistic analysis of Indo-Pacific hormurid scorpion phylogeny under implied weighting (IW) with  $K = 10$  that minimize length and maximize fit and branch support (length, 348 steps;  $F_i$ , 88.27%; average branch support, 46.8%). Zero length branches are collapsed under “rule 1”. Symmetric resampling frequencies (GC scores) of nodes indicated below corresponding branches.



Judging from the phylogenetic position of *Hormiops* (Fig. 5; [5]), from ecological observations in the field, and from the current knowledge of Sundaland geomorphological history during the Late Cretaceous and Cenozoic, the first scenario is regarded here as the preferred hypothesis. The evolution and distribution through time of *Hormiops* are considered here to be intricately correlated with the geomorphological history of Sundaland during the Late Cretaceous and Cenozoic. They probably resulted from drastic changes of palaeotopography and successive contractions/expansions of megathermal forests across the region. An ongoing biogeographic analysis based on molecular dating and ancestral areas reconstructions (Monod and Prendini, in prep.) will allow confirming whether the hypothesis formulated here is correct.

During the course of the present study, a detailed and comprehensive synthesis of Sundaland palaeogeography and palaeoenvironments from the Cretaceous onward was compiled from numerous publications on geology, palynology and palaeoclimatology. The evolution of Sundaland geomorphology through time involved numerous and complex events. Presenting all information necessary to fully understand these processes in the main text would make it difficult to read. Therefore, an overview is provided in the supplementary material and can be easily referred to by the readers.

#### 4.1. Occurrence of ancient arachnid lineages on the Côn Đảo and Seribuat Archipelagos

The Côn Đảo and Seribuat Archipelagos are remnants of a Late Cretaceous cordillera extending along the eastern Sundaland margin [40], and due to their continental origin, these islands harbour an array of arachnids belonging to primitive lineages. Five ancient taxa unrelated to *Hormiops* are known from the rainforests of Pulau Tioman [41–44], i.e. *Chaerilus sejnai* Kovařík, 2005, a scorpion of the basal family Chaerilidae Pocock, 1893 [45]; *Oncopus tiomanensis* Schwendinger & Martens, 2004, a humicolous harvestmen (Opiliones), representative of the Sandokanidae Özdikmen & Kury, 2005, a basal family of the sub-order Laniatores [46–48]; two undescribed species of the oldest opilionid sub-order Cyphophthalmi Simon, 1879 [47,48]; *Liphistius tioman* Platnick & Sedgwick, 1984, a burrowing spider of the archaic sub-order Mesothelae Pocock, 1892 [45,49]. Two chaerilid scorpions are thus far also reported from perhumid habitats of the Côn Đảo archipelago [8,50], i.e. *Chaerilus phami* Lourenço, 2011 and *Chaerilus terueli* Kovařík, 2012.

These primitive arachnids have putatively very limited dispersal capacities [51,52], a character shared by both *Hormiops* species. *H. davidovi* and *H. infulcra* sp. nov. are lithophilous species and, like many other Australasian hormurids [5,15,38,53], these stenotopic scorpions are arguably poor dispersers with a low tolerance to other substrates [36]. All these rainforests-restricted taxa, *Hormiops* included, can be considered as palaeoendemic elements, remnants of Sundaland's south-eastern mountains biota, and most likely evolved in response to the same vicariance events. Divergence of the two Tioman stylocellid mite-harvestmen from their mainland counterparts

at about 65 Ma [44] is congruent with this hypothesis and confirms the antiquity of these opilionids and their presence on the island before the formation of the Gulf of Thailand and of the South China Sea.

#### 4.2. Occurrence of *Hormiops* on the islands

Both the Côn Đảo and Seribuat Archipelagos are at least 80 Ma old [54–58] and were arguably part of ancient palaeomountains that existed from the Late Cretaceous until the Mid Eocene [40,56,59–74]. Therefore, when these islands became isolated from the mainland (probably in the Eocene–Oligocene) due to the subsidence of extensive land areas, the formation of various sedimentary basins and increasing marine transgressions [63,66,72,74–84] across the South China Sea region, they undoubtedly already carried an established flora and fauna, including hormurid scorpions. The presence of other hormurids with relatively similar ecological requirements on the islands would have prevented their colonization by *Hormiops*. It is commonly accepted that the first successful colonization of an island or island group inhibits subsequent settlements of closely related taxa through niche pre-emption and interspecific competition. Only species from distant lineages and with different ecological adaptations are potentially able to survive and establish perennial populations on an island already inhabited by closely related taxa [85–88].

Therefore, the recent colonization of either the Côn Đảo or Seribuat Archipelagos from the mainland by *Hormiops*, as well as dispersal from one to the other, is highly unlikely. Evidence rather suggests that the presence of *Hormiops* species on the islands is ancient, preceding the formation of the South China Sea Basin and of the Gulf of Thailand. It is interesting to emphasize here that the widespread species *L. australasiae* is found in syntopy with *H. infulcra* sp. nov. on Pulau Tioman. Ecology of the Tioman hormurids strongly suggests that the presence of *Hormiops* probably predates the dispersal of *L. australasiae* to the island. The eurytopic *L. australasiae* indifferently colonizes holes in tree trunks and crevices in rock faces, at least in places where other hormurids do not occur (L. Monod, unpublished). On Pulau Tioman, however, *L. australasiae* predominantly inhabits trees, and rarely occurs in rock crevices. *L. australasiae* is approximately the same size as *H. infulcra* sp. nov., and both species have overlapping microhabitat requirements. It is thus postulated here that the presence of *Hormiops* on the island restricted the niches available to *L. australasiae* to trees, a habitat rarely used by *H. infulcra* sp. nov., which prefers rocks (see description). It is probable that *L. australasiae* would have colonized trees and rocks alike if *H. infulcra* sp. nov. was not already present on the island.

#### 4.3. Ecology of *Hormiops*

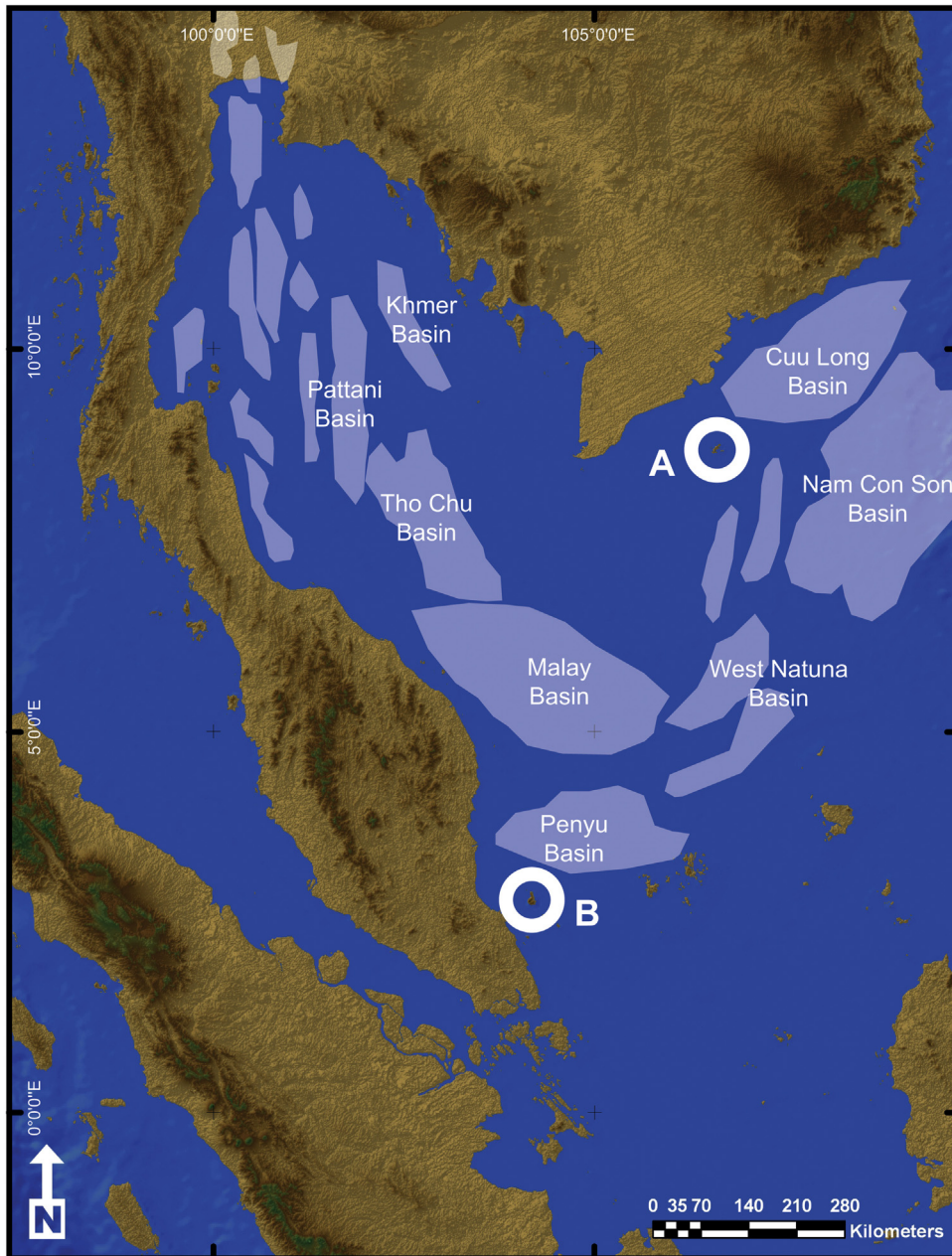
The common ancestors of Australasian hormurids (*Hormiops*, *Hormurus* and *Liocheles*) were arguably crack-dwelling (colonizing trees and rocks), eurytopic, and restricted to everwet ecosystems, whereas the more derived hormurids comprise a higher proportion of more

stenotopic taxa [5]. This indicates a transition from arboreal/lithophilous towards exclusively lithophilous or pelophilous ecomorphotypes.

The recent discovery of several stenotopic *Hormurus* from seasonally dry habitats of northern Australia [38] suggests that the decrease of tree density during phases of drier climates may be a preponderant factor responsible for the evolution of ecomorphological specializations, the corticolous scorpions seeking shelter and humidity on alternative substrates and eventually evolving specialized

behaviours and characters in response to selective pressures exerted by these new substrates (Monod et al., in prep.).

The morphology and microhabitat of *Hormiops* are extremely similar to that of the Australian *H. longimanus* and *Hormurus macrochela* Monod 2013. Although *Hormiops* occurs in much wetter ecosystems than the two Australian species, it is postulated here that its morphology has evolved in response to environmental conditions similar to those of the two Australian taxa, i.e. seasonally dry forests. Therefore, I believe that the current evergreen rainforests



**Fig. 6.** (Colour online.) Map of the Gulf of Thailand and South East China Sea Region showing the Côn Đảo (A) and Seribuat (B) archipelagos and the different sedimentary basins. All the basins started to develop in the Early Eocene as a result of faulting and rifting of the Sunda shelf, first forming an extensive network of palaeolakes in the Early Oligocene and finally becoming completely marine in the Middle to Late Miocene after Shoup et al. [70].

of Côn Đảo and Pulau Tioman were previously drier and the tree cover more open than today, at least episodically.

This hypothesis is congruent with the accepted Sundaland palaeoclimate model (see supplementary material). During the Late Eocene, Sundaland's everwet forests were largely replaced by subhumid vegetation types [62,72,80,84,89–93]. Moreover, palynological evidence from the West Natuna Basin even suggests that during the Oligocene floral communities in the South China Sea region shared some similarities with today's seasonally dry open woodlands of SE Queensland [72].

The occurrence of several pelophilous *Liocheles* species in Asia, e.g. *Liocheles nigripes* (Pocock, 1897) in northern India, and several undescribed species from Malaysia, Vietnam (L. Prendini, pers. com.), and Thailand (L. Monod, unpublished), as well as numerous lithophilous species in the ancient Laurasian scorpion lineage Scorpionidae Kraepelin, 1905 [94–98] suggest that the contraction of perhumid forests and the extension of drier vegetation types during the Cenozoic may have promoted the evolution of predominantly stenotopic scorpion lineages in continental South Asia.

#### 4.4. Evolution of *Hormiops* on Sundaland

It is postulated that, during the Late Cretaceous–Early Cenozoic, the tectonic exhumation of Sundaland [69,83], the climate and vegetation alteration at the K–Pg boundary [92,99–102], or more likely a combination of these two large-scale events, induced in the hormurid lineage a phase of allopatric diversification that was probably coupled with the extinction of many species, eventually leading to the divergence of the extant genera *Hormiops*, *Hormurus*, and *Liocheles*.

The uplift of an extensive peri-Sundaland cordillera in the Late Cretaceous [40,62,63,66,67,69,72,73,83] probably resulted in severe disruptions of the landscape and consequently in the fragmentation of ecosystems across the region. Biological responses to this tectonic rearrangements were probably also influenced by the climate and vegetation patterns. Floral communities were at the time rather diverse, from seasonally dry savannah in the north to perhumid rainforests in the south [62,72,92,93,103], and thus provided a wide range of habitats that may have facilitated ecological diversification. The K–Pg global deforestation abruptly altered these ecosystems, resulting in adverse environmental conditions and increasing ecological stresses on their biotas.

In the Mid Eocene, *Hormiops* had putatively already diverged from *Liocheles* by allopatric speciation/vicariance on Sundaland. Resumption of subduction at the margins [66,70] induced subsidence [63,66,74–76,78,79,83] and the formation of a fractured topography of horsts and grabens [62,63,72,83]. Furthermore, the expansion of sclerophyll vegetation in the Late Eocene (38–33 Ma) [62,72,80,84,89–93] resulted in the contraction of Southeast Asian everwet forests to Assam/Manmar [62,72,92,104] and to refugia along the southern and south-eastern coasts of Sundaland [62,72,92,93]. The landscape was then dominated by seasonally dry, open woodlands, and suitable habitat for humidity-dependent taxa such as hormurids

were drastically reduced on the Sunda shelf, probably restricted to uplands and coastal areas [72]. These climatic and tectonic alterations are likely to have significantly affected Asian hormurid scorpions, possibly promoting a second period of diversification and extinction that reduced the distribution range of *Hormiops* to south-eastern refugia in the Sundaland palaeocordilleras.

Land connections between the Côn Đảo and Seribuat archipelagos were finally severed in the Oligocene with the formation of the Gulf of Thailand and South China Sea sedimentary basins (Fig. 6) [63,72,77,78,80–84]. Development of these basins also led to a dramatic reduction of emergent land and thus to further reduction of suitable habitats, resulting in the isolation of *Hormiops* on two island groups of the South China Sea. The two known *Hormiops* species thus diversified by vicariance following the disjunction of the ancestral range of the genus and are considered here as palaeoendemics. It must be emphasized that *Hormiops* possibly also survives on other archipelagos of the South China Sea and in the granitic massifs of south-western Borneo, all of which are vestiges of ancient Sundaland mountain ranges. The genus has so far not been recorded from these regions, and more field work is needed to check for its presence.

#### Disclosure of interest

The authors declare that they have no conflicts of interest concerning this article.

#### Acknowledgements

Field work in Malaysia and Vietnam was funded in part by the MHNG. The author wishes to express his gratitude to the following persons:

- for granting access to the collections and preparing loans: Jacqueline Heurtault, Wilson Lourenço and Christine Rollard (MNHN), Lua Hui Keng, Peter Ng and Chang Man Wang (RMBR);
- for helping with the administrative procedure of getting collecting permits for the Côn Đảo National Park: Dinh Sac Pham;
- for providing scientific advice and constructive comments: Lorenzo Prendini and Peter Schwendinger;
- for identifying the salticid spider: Dmitri Logunov;
- for providing comments on an early draft of the manuscript: Peter Schwendinger;
- for providing critical comments that helped improve and clarify the manuscript: Camilo Mattoni and an anonymous reviewer;
- for assistance during fieldwork: Delphine Gaillard and Gwendolyn Romand.

#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crv.2014.07.009>.



## References

- [1] W.R. Lourenço, Rétablissement de la famille de Ischnuridae, distinctes des Scorpionidae Pocock, 1893, à partir de la sous-famille des Ischnurinae Pocock, 1893. *Rev. Arachnol.* 8 (1989) 159–177.
- [2] V. Fet, Family Ischnuridae Simon, 1879, in: V. Fet, W.D. Sissom, G. Lowe, M.E. Braunwalder (Eds.), *Catalog of the scorpions of the world (1758–1998)*, NY Entomological Society, New York, 2000, pp. 383–408.
- [3] W.R. Lourenço, L. Monod, Confirmation de la validité du genre *Hormiops* Fage, 1933 avec redescription d'*Hormiops davidovi* Fage, 1933 (Scorpiones, Ischnuridae), *Zoosystema* 21 (1999) 337–344.
- [4] L. Prendini, Phylogeny and classification of the superfamily Scorpionoidea Latreille, 1802 (Chelicerata, Scorpiones): an exemplar approach, *Cladistics* 16 (2000) 1–78.
- [5] L. Monod, L. Prendini, Evidence for Eurogondwana: the roles of dispersal, extinction and vicariance in the evolution and biogeography of Indo-Pacific Hormuridae (Scorpiones: Scorpionoidea), *Cladistics* (2014), <http://dx.doi.org/10.1111/cla.12067>.
- [6] L.L. Grismer, T.M. Youmans, P.L. Wood Jr., J.L. Grismer, Checklist of the herpetofauna of the Seribu Archipelago, West Malaysia with comments on biogeography, natural history, and adaptive types, *Raffles Bull. Zool.* 54 (2006) 157–180.
- [7] F. Kovařík, First record of *Liocheles nigripes* from Indonesia and Malaysia and *Hormiops davidovi* from Malaysia (Scorpiones: Ischnuridae), *Acta Soc. Zool. Bohem.* 64 (2000) 57–64.
- [8] W.R. Lourenço, Scorpions from the Island of Côn Sơn (Poulo Condore), Vietnam and description of a new species of *Chaerilus* Simon, 1877 (Scorpiones, Chaerilidae), *C. R. Biologies* 334 (2011) 773–776.
- [9] H.L. Stahnke, UV light, a useful field tool, *Bioscience* 22 (1972) 604–607.
- [10] A.D. Chapman, O. Grafton, Guide to best practices for generalising primary species-occurrence data, version 1.0, Global Biodiversity Information Facility, Copenhagen, 2008, Available at <http://www2.gbi-f.org/BPSensitiveData.pdf> (accessed 2011).
- [11] H.L. Stahnke, Scorpion nomenclature and mensuration, *Entomol. News* 81 (1970) 297–316.
- [12] M. Vachon, Étude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). 1. La trichobothriotaxie chez les scorpions, *Bull. Mus. Natl. Hist. Nat.* 140 (1974) 857–958.
- [13] H.W.C. Couzijn, Functional anatomy of the walking-legs of Scorpionida with remarks on terminology and homologization of leg segments, *Neth. J. Zool.* 26 (1976) 453–501.
- [14] B.H. Lamoral, The scorpions of Namibia (Arachnida: Scorpionida), *Ann. Natal Mus.* 23 (1979) 497–784.
- [15] L. Monod, E.S. Volschenk, *Liocheles litodactylus* (Scorpiones: Liochelidae): an unusual new *Liocheles* species from the Australian Wet Tropics (Queensland), *Mem. Queensl. Mus.* 49 (2004) 675–690.
- [16] W.P. Maddison, D.R. Maddison, Mesquite: a modular system for evolutionary analysis, version 2.75, 2011 Available at: <http://mesquiteproject.org> (accessed 2014).
- [17] W.M. Fitch, Toward defining the course of evolution: minimum change for a specific tree topology, *Syst. Zool.* 20 (1971) 409–416.
- [18] J.S. Farris, Method for computing Wagner trees, *Syst. Zool.* 19 (1970) 83–92.
- [19] K.C. Nixon, *Winclada* (Beta) ver. 0.9.9, Ithaca, NY, 1999.
- [20] P.A. Goloboff, Analyzing large data sets in reasonable times: solutions for composite optima, *Cladistics* 15 (1999) 415–428.
- [21] P.A. Goloboff, J.S. Farris, K.C. Nixon, T.N.T. Tree analysis using New Technology. Program and documentation, 2003 Available at <http://www.lillo.org.ar/phylogeny/tnt/> (accessed 2014).
- [22] P.A. Goloboff, J.S. Farris, K.C. Nixon, TNT, a free program for phylogenetic analysis, *Cladistics* 24 (2008) 774–786.
- [23] K.C. Nixon, The parsimony ratchet: a new method for rapid parsimony analysis, *Cladistics* 15 (1999) 407–414.
- [24] W.C. Wheeler, Sequence alignment, parameter sensitivity, and the phylogenetic analysis of molecular data, *Syst. Biol.* 44 (1995) 321–331.
- [25] P.A. Goloboff, Estimating characters weights during tree search, *Cladistics* 9 (1993) 83–91.
- [26] P.A. Goloboff, Self-weighted optimization: tree searches and character state reconstructions under implied transformation costs, *Cladistics* 17 (1997) 225–245.
- [27] D.L. Swofford, D.P. Beagle, PAUP phylogenetic analysis using parsimony, Version 3.1, User's manual, Illinois Natural History Survey, Champaign, Illinois, 1993.
- [28] J. Coddington, N. Scharff, Problems with zero-length branches, *Cladistics* 10 (1994) 425–433.
- [29] P.A. Goloboff, J.S. Farris, M. Källersjö, B. Oxelman, M.J. Ramírez, C.A. Szumik, Improvements to resampling measures of group support, *Cladistics* 19 (2003) 324–332.
- [30] L. Fage, Les scorpions de l'Indochine française, leur affinités, leur distribution géographique, *Ann. Soc. Entomol. Fr.* 102 (1933) 25–34.
- [31] L. Fage, Nouvelle contribution à l'étude des scorpions de l'Indochine française, *Bull. Soc. Entomol. Fr.* 41 (1936) 179–181.
- [32] A. Kästner, Ordnung der Arachnida: Scorpiones, in: W. Kükenthal, T. Krumbach (Eds.), *Handbuch der Zoologie*, Band 3, Häfte 2, Teil 1, Walter de Gruyter Verlag, Berlin, 1941, pp. 229–240.
- [33] H. Takashima, Scorpions of Eastern Asia, *Acta Arachnol.* 9 (1945) 68–106.
- [34] L. Fage, Scorpions et pédipalpes de l'Indochine française, *Ann. Soc. Entomol. France* 113 (1946) 71–81.
- [35] F. Kovařík, Štiří (Scorpions, Jihlava, Madagascar, 1998.
- [36] L. Prendini, Substratum specialization and speciation in southern African scorpions: the Effect Hypothesis revisited, in: V. Fet, P.A. Selden (Eds.), *Scorpions 2001*, In memoriam Gary A. Polis, British Arachnological Society, Burnham Beeches, Bucks, 2001, pp. 113–138.
- [37] International Union for the Conservation of Nature, (IUCN), IUCN Red List categories and criteria, Version 3.1, IUCN Species Survival Commission, IUCN, Gland, Cambridge, 2001, Available from: [http://www.iucnredlist.org/static/categories\\_criteria](http://www.iucnredlist.org/static/categories_criteria).
- [38] L. Monod, M.S. Harvey, L. Prendini, Stenotopic *Hormurus* Thorell, 1876 scorpions from the monsoon ecosystems of northern Australia, with a discussion on the evolution of burrowing behaviour in Hormuridae Laurie, 1896, *Rev. Suisse Zool.* 120 (2013) 281–346.
- [39] L.R. Rivas, A reinterpretation of the concepts “sympatric” and “allopatric” with proposal of the additional terms “syntopic” and “allo-topic”, *Syst. Biol.* 13 (1964) 42–43.
- [40] M. Pubellier, C.K. Morley, The basins of Sundaland (SE Asia): evolution and boundary conditions, *Mar. Pet. Geol.* (2013), <http://dx.doi.org/10.1016/j.marpetgeo.2013.11.019>.
- [41] N.I. Platnick, W.C. Sedgwick, A revision of the spider genus *Liphistius* (Aranea, Mesothelae), *Am. Mus. Novit.* 2781 (1984) 1–31.
- [42] P.J. Schwendinger, J. Martens, A taxonomic revision of the family Oncopodidae IV, The genus *Oncopus* Thorell (Opiliones, Laniatores), *Rev. Suisse Zool.* 111 (2004) 139–174.
- [43] F. Kovařík, Two new species of the genus *Chaerilus* Simon, 1877 from Malaysia (Scorpiones: Chaerilidae), *Euscorpium* 26 (2005) 1–9.
- [44] R.M. Clouse, G. Giribet, When Thailand was an island—the phylogeny and biogeography of mite harvestmen (Opiliones, Cyphophthalmi, Stylocellidae) in Southeast Asia, *J. Biogeogr.* 37 (2010) 1114–1130.
- [45] J.A. Coddington, G. Giribet, M.S. Harvey, L. Prendini, D.E. Walter, Arachnida, in: J. Cracraft, M.J. Donoghue (Eds.), *Assembling the tree of life*, Oxford University Press, New York, 2004, pp. 296–318.
- [46] J.W. Shultz, Phylogeny of Opiliones (Arachnida): an assessment of the ‘Cyphopalpatores’ concept, *J. Arachnol.* 26 (1988) 257–272.
- [47] G. Giribet, G.D. Edgecombe, W.C. Wheeler, C. Babbitt, Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data, *Cladistics* 18 (2002) 5–70.
- [48] G. Giribet, L. Vogt, A.P. González, P. Sharma, A.B. Kury, A multilocus approach to harvestmen (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores, *Cladistics* 26 (2010) 408–437.
- [49] R.F. Foelix, *Biology of spiders*, Second Edition, Oxford University Press, New York, 1996.
- [50] F. Kovařík, Five new species of *Chaerilus* Simon, 1877 from China, Indonesia, Malaysia, Philippines, Thailand, and Vietnam (Scorpiones: Chaerilidae), *Euscorpium* 149 (2012) 1–14.
- [51] W.S. Bristowe, The liphistiid spiders, *Proc. Zool. Soc. Lond.* 4 (1932) 1015–1057.
- [52] G. Giribet, A.B. Kury, Phylogeny and biogeography, in: R. Pinto-da-Rocha, G. Machado, G. Giribet (Eds.), *Harvestmen: the biology of Opiliones*, Harvard University Press, Cambridge, MA, USA, 2007, pp. 62–87.
- [53] L. Monod, Taxonomic emendations in the genus *Liocheles* Sundevall, 1833 (Scorpiones, Liochelidae), *Rev. Suisse Zool.* 118 (2011) 723–758.
- [54] T.W.C. Hilde, C. Engel, Age, composition, and tectonic setting of the granite island, Hon Trung Lon, off the coast of South Vietnam, *Geol. Soc. Am. Bull.* 78 (1967) 1289–1294.
- [55] J.D. Bignell, N.J. Snelling, R.R. Harding, *Geochronology of Malayan Granites*, Overseas Geology and Mineral Resources 47, The Stationery Office, London, 1978.
- [56] T.T.B. Nguyen, M. Satir, W. Siebel, S. Chen, Granitoids in the Dalat zone, southern Vietnam: age constraints on magmatism and regional geological implications, *Int. J. Earth Sci.* 93 (2004) 329–340.

- [57] N.T.B. Thuy, M. Satir, W. Siebel, T. Venneman, T.V. Long, Geochemical and isotopic constraints on the petrogenesis of granitoids from the Dalat zone, southern Vietnam, *J. Asian Earth Sci.* 23 (2004) 467–482.
- [58] M.P. Searle, M.J. Whitehouse, L.J. Robb, A.A. Ghani, C.S. Hutchison, M. Sone, S.W.-P. Ng, M.H. Roselee, S.-L. Chung, G.J.H. Oliver, Tectonic evolution of the Sibumasu–Indochina terrane collision zone in Thailand and Malaysia: constraints from new U–Pb zircon chronology of SE Asian tin granitoids, *J. Geol. Soc. London* 169 (2012) 489–500.
- [59] B.-M. Jahn, P.Y. Chen, T.P. Yen, Rb–Sr ages of granitic rocks in southeastern China and their tectonic significance, *Geol. Soc. Am. Bull.* 87 (1976) 763–776.
- [60] B. Taylor, D.E. Hayes, D.E., Origin and history of the South China Sea Basin, in: D.E. Hayes (Ed.), *The tectonic and geologic evolution of Southeast Asian seas and islands, Part 2, Geophys. Monogr. 27, American Geophysical Union, Washington DC, 1983, pp. 23–56.*
- [61] B.-M. Jahn, X.H. Zhou, J.L. Li, Formation and tectonic evolution of the SE China and Taiwan: isotopic and geological constraints, *Tectonophysics* 183 (1990) 145–160.
- [62] R.J. Morley, *Origin and evolution of tropical rain forests*, Wiley & Sons, London, 2000.
- [63] R. Hall, C.K. Morley, Sundaland Basins, in: P. Clift, P. Wang, W. Kuhnt, D.E. Hayes (Eds.), *Continent–Ocean Interactions within the East Asian Marginal Seas, Geophys. Monogr. 149, American Geophysical Union, Washington DC, 2004, pp. 55–85.*
- [64] Z.-X. Li, X.-H. Li, Formation of the 1300 km-wide intracontinental orogeny and postorogenic magmatic province in Mesozoic South China: a flat-slab subduction model, *Geology* 35 (2007) 179–182.
- [65] D. Zhou, Z. Sun, H. Chen, H. Xu, W. Wang, X. Pang, D. Cai, D. Hu, Mesozoic palaeogeography and tectonic evolution of South China Sea and adjacent areas in the context of Tethyan and Paleo-Pacific interconnections, *Isl. Arc* 17 (2008) 186–207.
- [66] R. Hall, Hydrocarbon basins in SE Asia: understanding why they are there, *Pet. Geosci.* 15 (2009) 131–146.
- [67] R. Hall, B. Clements, H.R. Smyth, Sundaland: basement character, structure and plate tectonic development, in: *Proceedings of the 33rd Annual Convention of the Indonesian Petroleum Association, 2009, pp. 1–27.*
- [68] M.B.W. Fyhn, S.A.S. Pedersen, L.O. Boldreel, L.H. Nielsen, P.F. Green, P.T. Dien, L.T. Huyen, D. Frei, Palaeocene–Early Eocene inversion of the Phuquoc–Kampot Som Basin: SE Asian deformation associated with the suturing of Luconia, *J. Geol. Soc. London* 167 (2010) 281–295.
- [69] B. Clements, P.M. Burgess, R. Hall, M.A. Cottam, Subsidence and uplift by slab-related mantle dynamics, a driving mechanism for the Cretaceous and Cenozoic evolution of continental SE Asia? in: R. Hall, M.A. Cottam, M.E.J. Wilson (Eds.), *The SE Asian gateway: history and tectonics of the Australia–Asia collision, Geological Society Special Publication 355, Geological Society, London, 2011, pp. 37–51.*
- [70] R. Hall, Late Jurassic–Cenozoic reconstructions of the Indonesian region and the Indian Ocean, *Tectonophysics* 570–571 (2012) 1–41.
- [71] C.K. Morley, Late Cretaceous–Early Palaeogene tectonic development of SE Asia, *Earth Sci. Rev.* 115 (2012) 37–75.
- [72] R.J. Morley, A review of the Cenozoic palaeoclimate history of Southeast Asia, in: D.J. Gower, K.G. Johnson, J.E. Richardson, B.R. Rosen, L. Rüber, S.T. Williams (Eds.), *Biotic evolution and environmental change in SE Asia, Cambridge University Press, Cambridge, 2012, pp. 79–114.*
- [73] R. Hall, The palaeogeography of Sundaland and Wallacea since the Late Jurassic, *J. Limnol.* 72 (2013) 1–17.
- [74] S. Zahirovic, M. Seton, R.D. Müller, The Cretaceous and Cenozoic tectonic evolution of Southeast Asia, *Solid Earth Discuss.* 5 (2013) 1335–1422.
- [75] P. Molnar, P. Tapponnier, Cenozoic tectonics of Asia: effects of a continental collision, *Science* 189 (1975) 419–426.
- [76] P. Tapponnier, G. Peltzer, R. Armijo, On the mechanism of collision between India and Asia, in: M.P. Coward, A.C. Ries (Eds.), *Collision Tectonics, Geological Society Special Publication 19, Geological Society, London, 1986, pp. 115–157.*
- [77] J.M. Cole, Freshwater dinoflagellate cysts and acritarchs from Neogene and Oligocene sediments of the South China Sea and adjacent areas, in: J.M. Head, J.H. Wrenn (Eds.), *Neogene and Quaternary dinoflagellate cysts and acritarchs, American Association of Stratigraphic Palynologists Foundation, Dallas, 1992, pp. 181–196.*
- [78] J.M. Cole, S. Crittenden, Early Tertiary basin formation and the development of lacustrine and quasi-lacustrine/marine source rocks on the Sunda Shelf of SE Asia, in: A.J. Fraser, S.J. Matthews, R.W. Murphy (Eds.), *Petroleum Geology of Southeast Asia, Geological Society Special Publication 126, Geological Society, London, 1997, pp. 147–183.*
- [79] P.H. Leloup, N. Arnaud, R. Lacassin, J.R. Kienast, T.M. Harrison, T.T.P. Trong, A. Replumaz, P. Tapponnier, New constraints on the structure, thermochronology, and timing of the Ailao Shan–Red River shear zone, SE Asia, *J. Geophys. Res.* 106 (2001) 6683–6732.
- [80] R.J. Morley, H.P. Morley, P. Restrepo-Pace, Unraveling the tectonically controlled stratigraphy of the West Natuna Basin by means of palaeo-derived Mid Tertiary climate changes, in: *Proceedings of the 29th Annual Convention of the Indonesian Petroleum Association, 2003, pp. 1–24.*
- [81] R.J. Morley, P. Salvador, M.L. Challis, W.R. Morris, I.R. Adyaksawan, Sequence biostratigraphic evaluation of the North Belut Field, West Natuna Basin, in: *Proceedings of the 31st Annual Convention of the Indonesian Petroleum Association, 2007, pp. 357–376.*
- [82] R.J. Morley, T. Swiecicki, D.T.T. Pham, A sequence stratigraphic framework for the Sunda region, based on biostratigraphic, lithological and seismic data from Nam Côn Sơn Basin, Vietnam, in: *Proceedings of the 35th Annual Convention of the Indonesian Petroleum Association, 2011, pp. 1175–1196.*
- [83] M.A. Cottam, R. Hall, A.A. Ghani, Late Cretaceous and Cenozoic tectonics of the Malay Peninsula constrained by thermochronology, *J. Asian Earth Sci.* 76 (2013) 241–257.
- [84] R.C. Shoup, R.J. Morley, T. Swiecicki, S.J. Clark, Tectono-stratigraphic framework and Tertiary paleogeography of Southeast Asia: gulf of Thailand to South Vietnam shelf, *Houston. Geol. Soc. Bull.* 55 (2013) 27–39.
- [85] G. Hormiga, M. Arnedo, R.G. Gillespie, Speciation on a conveyor belt: sequential colonization of the Hawaiian islands by *Orsonwelles* spiders (Araneae, Linyphiidae), *Syst. Biol.* 52 (2003) 70–88.
- [86] R.G. Gillespie, Community assembly through adaptive radiation in Hawaiian spiders, *Science* 303 (2004) 356–359.
- [87] J. Silvertown, The ghost of competition past in the phylogeny of island endemic plants, *J. Ecol.* 92 (2004) 168–173.
- [88] J.E. Garb, R.G. Gillespie, Island hopping across the Central Pacific: mitochondrial DNA detects sequential colonization of the Austral Islands by crab spiders (Araneae: Thomisidae), *J. Biogeogr.* 33 (2006) 201–220.
- [89] A.M. Yakzan, H. Awalludin, M.N. Bahari, R.J. Morley, Integrated biostratigraphic zonation for the Malay Basin, *Bull. Geol. Soc. Malaysia* 39 (1996) 157–184.
- [90] A. Carnell, P. Butterworth, B. Hamid, A. Livsey, J. Barton, C. Bates, The brown shale of Central Sumatra, A detailed geological appraisal of a shallow lacustrine source rock, in: *Proceedings of the 26th Annual Convention of the Indonesian Petroleum Association, 1998, pp. 51–69.*
- [91] R.J. Morley, J. Shamsuddin, The sequence biostratigraphy and chronostratigraphy of the Malay Basin, in: *Geological Society of Malaysia (Ed.), Petroleum Geology Conference & Exhibition, Kuala Lumpur, Malaysia, 27–28 November 2006: Unravelling Malaysia's exploration potential through latest technology and ideas, Program and Abstracts, Geological Society of Malaysia, Kuala Lumpur, 2006, p. 77.*
- [92] R.J. Morley, Cretaceous and Tertiary climate change and the past distribution of megathermal rain forests, in: M. Bush, J.R. Flenley (Eds.), *Tropical rainforest responses to climatic change, Springer-Praxis, Berlin–Chichester, 2006, pp. 1–26.*
- [93] E.B. Lelono, R.J. Morley, Oligocene palynological succession from the East Java Sea, in: R. Hall, M. Wilson (Eds.), *The SE Asian gateway: history and tectonics of the Australia–Asia collision, Geological Society Special Publication 355, Geological Society, London, 2011, pp. 333–345.*
- [94] F. Kovařík, *Euscorpions thaomischii* sp. n. from Vietnam and a key to species of the genus *Euscorpiones: Euscorpidae: Scorpiopinae*, *Euscorpion* 142 (2012) 1–10.
- [95] F. Kovařík, *Alloscorpions wrongpromi* sp. n. from Thailand and Laos (Scorpiopinae: Euscorpidae: Scorpiopinae), *Euscorpion* 160 (2013) 1–14.
- [96] W.R. Lourenço, A new species of *Euscorpions* Vachon, 1980 from Laos (Scorpiopinae: Euscorpidae: Scorpiopinae), *Acta Arachnol.* 62 (2013) 23–27.
- [97] W.R. Lourenço, D.S. Pham, First record of a cave species of *Euscorpions* Vachon from Viet Nam (Scorpiopinae, Euscorpidae, Scorpiopinae), *C. R. Biologies* 336 (2013) 370–374.
- [98] Z.A. Mirza, R.V. Sanap, R. Upadhye, A new species of scorpion of the genus *Neoscorpions* Vachon, 1980 (Scorpiopinae: Euscorpidae) from India, *C. R. Biologies* 337 (2014) 143–149.
- [99] R.H. Tschudy, C.L. Pillmore, C.J. Orth, Disruption of the terrestrial plant ecosystem at the Cretaceous–Tertiary boundary, Western Interior, *Science* 225 (1984) 1030–1032.
- [100] J.A. Wolfe, G.R. Upchurch Jr., Vegetation, climatic and floral changes at the Cretaceous–Tertiary boundary, *Nature* 324 (1986) 148–152.
- [101] V. Vajda, J.I. Raine, C.J. Hollis, Indication of global deforestation at the Cretaceous–Tertiary boundary by New Zealand fern spike, *Science* 294 (2001) 1700–1702.
- [102] A. Ocampo, V. Vajda, E. Buffetaut, Unravelling the Cretaceous–Paleogene (KT) turnover, evidence from flora, fauna and geology, in: C. Cockerell, C. Koeberl, I. Gilmour (Eds.), *Biological processes associated with impact events, Springer, Berlin, Heidelberg, 2006, pp. 197–219.*
- [103] P.J.E. Bransden, S.J. Matthews, A stratigraphic and structural evolution of the East Java Sea, Indonesia, in: *Proceedings of the 21st Annual Convention of the Indonesian Petroleum Association, 1992, pp. 418–453.*
- [104] N. Awasthi, R.C. Mehrotra, Oligocene flora from Makum Coalfield, Assam, India, *Palaeobotanist* 44 (1995) 157–188.