

A review and key to the genus *Phenacephorus* Brunner (Insecta: Phasmida: Heteronemiidae: Lonchodinae), including the description of two new species

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The genus *Phenacephorus* Brunner, 1907 is reviewed. Keys are provided for both males and females. Two new species from Borneo are described and illustrated. Eggs of three species are formally described for the first time. All five known species are partly illustrated and the synonymy of all species is given.

Introduction

The genus *Phenacephorus* was first described in 1907 by Brunner von Wattenwyl (hereafter referred to as Brunner). When the genus was described, Brunner included one previously described species, *P. verrucosus* (de Haan, 1842), and described two new species, *P. appendiculatus* and *P. cornucervi*. At that time males were unknown and the only known females were the three holotypes.

Since 1907, Brunner's two species have been found to be synonyms (Hausleithner, 1985) and a new species, *P. spinulosus* (Hausleithner, 1991), has been described. The females of three species and the males of two of the species have now been described, as has the egg of *P. spinulosus*.

This paper describes and illustrates two new species and their eggs, and gives a formal description of the egg of *P. cornucervi*. A complete synonymy is given for each species. The phylogeny of the genus is also considered.

Material and methods

In 1990 a collection of Phasmida was made in the area surrounding the Head Quarters of Mt Kinabalu Park, Sabah. The collection was made using head torches to search the vegetation at night. Two species, *P. cornucervi* and *P. spinulosus*, were collected and both were subsequently bred in captivity in the U.K. Further specimens of these two species were recorded at the same locality in August 1992.

A second collection of Phasmida was made in the Sepilok Forest Reserve, near Sandakan, Sabah, during August 1992; including a single female specimen of a new species of *Phenacephorus*. The specimen was kept alive for several days and laid five eggs. Four of these eggs were incubated and two subsequently hatched. Three further specimens of this species were identified in the collection at the Nationaal Natuurhistorisch Museum (RMNH), Leiden, Netherlands, during a visit in February 1993.

Günther (1943: 154) gave brief descriptions of what he believed to be two females

and two males of *P. verrucosus*. These four specimens were examined and compared with the holotype at RMNH and were found to be a distinct species. There is no evidence in the RMNH records that Günther ever examined the holotype of *P. verrucosus*.

Measurements in table 1 include wild caught and captive bred material in the author's collection, as well as previously published data. Specimens collected or reared by the author are given individual accession numbers which are preceded by the author's initials and a hyphen e.g. PEB-1234. Standard codens (Arnett, et al., 1993) are used to refer to the following institutions: Natural History Museum, Wien, Austria (NHMW), Forest Research Centre, Sandakan, Sabah, Malaysia (FRCS), National Museum of Natural History, Leiden, Netherlands (RMNH), Natural History Museum, London, UK (BMNH) and Natural History Museum, Nottingham, UK (NHMN). In addition DCMD is used to refer to Derby City Museum, Derby, UK. The eggs are described using the standard terminology as defined by Clark (1976). All type specimens have been examined.

Taxonomy

Phenacephorus Brunner, 1907

Phenacephorus Brunner, 1907: 291. Type species [here selected]: *P. cornucervi* Brunner, 1907.

P. cornucervi is selected as the type species because there are numerous specimens available for examination in various museums, both wild caught and captive reared. Of the other species placed in the genus by Brunner, one is a synonym of *P. cornucervi* and the other is known only from the holotype.

The genus can be shown to belong to the family Heteronemiidae, subfamily Lonchodinae, and tribe Lonchodini, by use of the keys provided by Bradley & Galil (1977); although allowance must be made for the errors in the keys, notably the use of mesonotum in mistake for the median segment in the key to the Heteronemiidae. The genus may be distinguished from other Lonchodini by the following combination of characteristics:

- a) The middle femora is shorter than the combined length of the metanotum and median segment in the females, and no longer than the combined length in the males.
- b) There is a lobe on the upper surface of the middle femora of the females; in the males this may be no more than a minute bump and may go unnoticed or it may be an obvious spine-like lobe.
- c) The back of the head is conical and tuberculate, or the females have obvious crests or lobes on the head and males have spines or noticeable tubercles on the head.

The genus is closest to *Lonchodes* Gray, 1835. The two genera are distinguished by the features on the head. Table 1 gives the lengths of the various species of *Phenacephorus*.

Description of the females

Back of the head at least slightly swollen or greatly swollen conical. Prominent lobes present either between the eyes, or on the back of the head, or both (figs. 10-

15). Median segment less than half the length of the metanotum. All femora short; the middle femora with at least one lobe (often foliaceous) on the upper surface (figs. 19-21). Abdomen usually with large tubercles or lobes on the dorsal surface.

Table 1. Variation in body length of the species of *Phenacephorus* (* paratype not fully developed).

Species	Female (mm)	Male (mm)
<i>P. cornucervi</i>	71-89	60-70
<i>P. spinulosus</i>	56.0-60.5	49.5-51.0
<i>P. verrucosus</i>	82	not known
<i>P. nieuwenhuisi</i> spec. nov.	(85*)-104	90
<i>P. sepilokensis</i> spec. nov.	96-108	not known

Description of the males

Head with two spines or large tubercles between the eyes. Back of the head flat, or raised and armed with 2-4 blunt spines or tubercles (figs. 16-18). Median segment much shorter than the metanotum. Middle femora no longer than the combined length of the metanotum and median segment. Middle femur with either an obvious angular lobe on the upper surface or a minute rounded bulge in the upper internal carina (figs. 22-24). Abdominal segments 7-9 widened (especially segments 8 and 9), forming an almost quadrangular structure.

Key to females of the genus *Phenacephorus*

1. Back of the head rounded and smooth, or with tubercles, not conical and without lobes. Between the eyes are large lobes which are simple, not serrated 2
 - Back of head with large backward pointing lobes or crests. Between the eyes are small serrated lobes or blunt spines 3
2. Middle femora and middle tibiae with only simple lobes which are not serrated *P. spinulosus* (Hausleithner, 1991)
 - Middle femora and middle tibiae with complex, serrated lobes *P. verrucosus* (de Haan, 1842)
3. Back of prothorax with spines or lobes or crests. Fore femora and fore tibiae with obvious wide, serrated foliaceous expansions running along their length 4
 - Prothorax smooth, fore femora with only narrow foliaceous expansions along their length *P. nieuwenhuisi* spec. nov.
4. A single pair of narrow lobes on the back of the head, pointing backwards. (Body length 90-108 mm) *P. sepilokensis* spec. nov.
 - Multiple lobes or crests on the back of the head, or a pair of large, wide lobes. (Body length 70-90 mm) *P. cornucervi* Brunner, 1907

Key to males of the genus *Phenacephorus*

1. Middle femora with an obvious angular lobe on the upper surface. Without obvious spines on the hind margin of each of the first six abdominal segments 2

- Middle femora with no more than a slightly raised curve on the upper internal carina of the middle femora. Prominent blunt spines on at least the first six abdominal segments *P. spinulosus* (Hausleithner, 1991)
 - 2. Two small spines, or at least a pair of obvious tubercles on the back edge of the pronotum. Body length less than 80 mm *P. cornucervi* Brunner, 1907
 - Back edge of the pronotum without any spines or obvious tubercles. Body length greater than 80 mm *P. nieuwenhuisi* spec. nov.
- N.B. The males of *P. sepilokensis* and *P. verrucosus* are unknown.

Phenacephorus cornucervi Brunner, 1907

Phenacephorus cornucervi Brunner, 1907: 292 (holotype ♀, Kina Balu (NHMW)); Günther, 1932: 314; Hausleithner, 1985: 315-319, 1987: 273-288; Raper, 1987: 13-14; Sellick, 1988: 273, fig. 3j; Hausleithner, 1991: 235; Bragg, 1992a: 191, fig. 5c, 1992b: 25.

Phenacephorus appendiculatus Brunner, 1907: 291, pl. XIII fig. 4 & 4a (holotype ♀, Kina Balu (NHMW)); Deschandol, 1986: 3. Synonymised by Hausleithner, 1985: 315.

The female of this species is highly variable, to the extent that the author has not seen two identical females although over 100 specimens have been reared to adult from a small gene pool consisting of two males and two females. Many of the variations have been described and illustrated by Hausleithner (1987). In contrast, the males exhibit little variation.

While both the crests on the head, and the lobes on the mid femur show considerable variation, figures 13 and 21 are typical examples and are included for comparison with those of other species. Having examined the holotypes of *P. cornucervi* and *P. appendiculatus*, and a series of captive bred material, there is no doubt that the synonymy (Hausleithner, 1985) is correct.

The egg (figs. 8 & 9).— Sellick (1988: fig. 3j) illustrated only the operculum while Hausleithner (1985: 317) and Raper (1987: 14) illustrated only the lateral view of the egg. No measurements have been recorded other than "3 mm long" (Raper, 1987: 14). The following data is taken from eggs laid by captive reared specimens; eggs laid by wild caught females were found to fall within these ranges.

Length 2.7-3.1 mm, height 2.2-2.6 mm, width 1.7-2.0. The mass of 121 freshly laid eggs (0-2 weeks old) was found to range from 5.14-7.34 mg with a mean of 6.40 mg and a standard deviation of 0.427. Opercular angle about -20°.

Capsule almost cuboid, with a large polar mound. The egg has 30-50 deep indentations in the surface and is densely covered in short fibres except for a small area at the bottom of most indentations. The capsule, operculum and micropylar plate are a uniform dark or mid brown, rarely light brown; occasional eggs occur which are mid brown on one half and dark brown on the other. The position of the micropylar plate is marked by a long thin oval which is slightly wider at the polar end, the fibrous covering of the egg obscures the details of its structure. The operculum is almost circular and has a capitular structure in the centre.

Although both Raper (1987: 14) and Sellick (1988: 278) state that the egg has a capitulum, the structure is not a capitulum typical of the Lonchodini in the sense that it is not a rounded, orange or yellow structure on a capitular stalk. The structure is fibrous, with the strands aligned with the axis of the egg, although longer, the fibres

appear to be the same as those covering the whole of the capsule. After soaking in dilute (0.05 M) potassium hydroxide solution, the fibres, on all parts of the capsule, can be removed by careful scraping without causing any obvious damage to the integrity of the capsule. When the fibres are removed from the operculum, a small capitular stalk is revealed, similar to the stalk left by the removal of a typical *Lonchodini* capitulum. Sellick (personal communication, June 1993) considers that this structure should be considered a capitulum because it softens in dilute (0.05 M) potassium hydroxide solution and may then be removed.

Phenacephorus spinulosus (Hausleithner, 1991)

Phasgania spinulosa Hausleithner, 1991: 230, figs. 9 & 10a-d (holotype ♂, Sabah, 32 mile, Sinsuran, coll. C.L. Chan & L. Chin, 17-08-1981 (NHMW)).

Phenacephorus spinulosus; Bragg, 1991: 3, 1992a: 185-192, 1993: 41-44

The combination of a lobed mid femur and lobes on the head (fig. 14) places this species in *Phenacephorus* although the back of the head is not conical and the mid femoral lobes are simple. The eggs are similar to those of many *Lonchodes* and *Carausius*, with a capitulum typical of the tribe rather than that of the type species. The species has been fully illustrated and the generic placement discussed in more detail elsewhere (Bragg, 1992a).

Phenacephorus verrucosus (de Haan, 1842)

Phasma (Acanthoderus) verrucosum de Haan, 1842: 136, pl. 14.1 (holotype ♀, Sumatra, Batang Singalang (RMNH)).

Prisomera verrucosum; Westwood, 1859: 48.

Hermogenes verrucosus; Kirby, 1896: 456, 1904: 322.

Phenacephorus verrucosus; Brunner, 1907: 291.

[*Phenacephorus verrucosus*, Günther, 1943: 154. Incorrect identification].

The only known specimen of this species is the holotype; Günther's reference to this species, and description of the male, was due to misidentification (see *P. nieuwenhuisi*, below). Examination of the holotype has shown de Haan's illustrations to be accurate. De Haan's illustration of the head is reproduced here (fig. 15) for comparison with those of the other species.

The type specimen was examined with a view to removing an egg. However the abdomen is flattened and it is unlikely that there are eggs present in the body cavity.

This species may be distinguished from the females of *P. cornucervi*, to which it is very closely related, by the shape and aspect of the lobes on the back of the head and by the size and shape of the eggs. The possibility that this is a lowland form of *P. cornucervi* was considered and rejected after comparison of the eggs (figs. 4-5 and 8-9) and after consideration of the limited variation in the specimens available. *P. cornucervi* is so variable that no two identical specimens have yet been found.

The eggs are considered to be of particular value in defining this species; those laid by the holotype, along with 25 eggs from the paratype (PEB-2028), are considered type material. All eggs are mounted in gelatin capsules.

The description of the colouration is based on the preserved material, the living captive reared specimens and a photographic transparency of the holotype which was taken, in situ, at the time of capture.

Description of the female (figs. 1, 10, 20).— Measurements of the adults are given in table 2. The head and body lengths of the individual specimens are: holotype 104 mm, Sieber's adult 96 mm, captive reared adult 108 mm.

Legs and bodies of preserved specimens are various shades of brown with some white or at least pale markings on the pronotum and front of the mesonotum.

Body and legs of living holotype with a base colour of mid brown; large tubercles on the body dark green, and legs mottled with pale brown. Pronotum and front quarter of the mesonotum, the two basal segments of the antennae, and 11th abdominal segment white. Middle and hind femora pale brown at the apices and bases, with small white markings about one third of the way from the base. Antennae pale with dark rings.

At second instar (33 mm), the captive reared specimens were pale brown with a green head, pronotum, and abdominal tubercles. At fourth instar (55 mm) the larger of the two nymphs was pale brown with darker speckles, apart from the pronotum and front of the mesonotum which were cream coloured. The colouration of the latter specimen was retained when adult, in addition there was a green spot on each side of the lateral margin of the mesonotum, just above the base of the mid femora, and a large orangy-pink patch on each side of the fifth abdominal segment.

The whole of the head, body and legs are granulose. Thorax, abdomen and lobes on legs rugose.

Two small spine like lobes between the eyes. Back of the head conical and crowned with two small backward pointing irregular lobes. Antennae indistinctly segmented, longer than the front legs. Basal segments flattened and widened, second segments almost as wide as long and twice as wide as the remainder.

Pronotum with a transverse depression midway along. Back of the pronotum with two triangular lobes which point forwards.

Mesonotum with numerous tubercles, two of which take the form of small irregular lobes. Narrow at the front, widening rapidly, almost uniform width for the last two thirds of its length.

Metanotum fused to median segment, both of uniform width. Metanotum with numerous tubercles. Median segment about one quarter of the length of the metanotum. Median segment of some paratypes with large tubercle or lobe on the hind margin.

Abdomen rugose and tuberculate. Hind margin of second segment with two

long, backward pointing triangular lobes, or a foliaceous tubercle. Large lobe like tubercles on hind margin of third, fifth and eighth segments; that on the fifth segment may be an exceptionally large curved lobe up to 5 mm high. Seventh segment with two long thin lobes projecting upwards, or occasionally a lobe like tubercle. Segments nine and ten short, with large lobes in the case of one paratype. Eleventh segment either three times longer than wide, forming a triangular process with irregular sides, or a short, blunt triangle.

Underside of thorax granulose and tuberculate. Underside of abdomen rugose.

Operculum very rugose and tuberculate, with an indistinct, irregular keel. Operculum only slightly longer than tenth segment.

All femora with spine-like lobes on the underside near the apices. All femora and tibiae rugose.

Fore femora narrow and incurving at the base. The upper surface has a triangular lobe running from the base, widening out and stopping abruptly two thirds of the way along. The fore tibiae have a finely serrated foliaceous expansion in the form of a long, thin lobe running along the upper surface; the lobes begin one sixth of the way along the tibiae and narrow suddenly as they reach the apices.

Mid femora are strongly thickened and have a large lobe on the upper surface. This lobe has an irregular margin and runs for more than half the length of the femora. Height of lobe greater than height of the femur. Mid tibiae with two irregular lobes on the upper surface; the first one third of the way along, the second at the apices.

Hind femora compressed. Hind legs simple, unarmed except for the small lobes on the underside of the femoral apices.

All tibiae short, front tibiae with a small lobe on the first tarsomere, others without lobes.

The egg (figs. 4 & 5).— The dimensions of five eggs were found to be: length 4.2-4.3 mm, width 2.1mm and height 2.8-2.9 mm. The mass, when freshly laid, ranged from 16.32-17.25 mg with a mean value of 16.74 mg and a standard deviation of 0.33. Opercular angle about -18° .

Capsule, micropylar plate, and operculum all uniform dark brown. Surface of capsule uneven and granular throughout. Micropylar plate almost rectangular and appears to be recessed into the surface of the egg. Micropylar plate with a high, central, longitudinal ridge leading to the micropyle at the polar end. A median line runs from the micropyle to the prominent polar body. Operculum oval, with a raised rim and irregular radial ridges. Centre of operculum bearing a capitular structure. When the egg is soaked in 0.5 M potassium hydroxide solution the outer, slightly fibrous, covering of the operculum softens and can be scraped off, revealing a capitular stalk similar to that of the type species.

Three days after hatching, nymphs were 20.5 mm long.

P. nieuwenhuisi spec. nov.

Phenacephorus verrucosus; Günther, 1943: 154 (not de Haan, 1842).

Material.— Holotype, ♀ (RMNH), Borneo, Mahakam, 1894, Borneo expedition of Dr Nieuwenhuis. Paratypes: 2♂♂ (RMNH), data as holotype; ♀ (RMNH), Borneo, Long Bloe-oe, Nov. 1898, Borneo expedition of Dr Nieuwenhuis.

The description and notes by Günther (1943: 154) are inaccurate and misleading; this species differs greatly from *P. verrucosus*. It lacks the large head lobes of *P. verrucosus* and has a conical mound on the back of the head.

Description of the female (figs. 2, 11, 12, 19).— The holotype is clearly a mature adult; however the legs and body of the female paratype are flattened and distorted in a manner which suggests that it had just completed ecdysis when it died. Measurements given in table 2 refer only to the holotype.

Holotype uniform mid brown, except for a wide longitudinal lighter brown stripe on abdominal segments 8-10. Female paratype almost uniform dark brown, almost black. Whole of body, head, and legs, densely granulose. Paratype with a few tubercles on the mesonotum and metanotum.

Head narrows slightly behind the eyes. Between the eyes are a small pair of spine-like lobes. Back of the head rises forming a high, finely tuberculate, conical mound (figs. 11 and 12). Antennae longer than the fore tibiae, indistinctly segmented, uniform thickness beyond the second segment. Basal segment broad and flattened, second segment almost as wide as long.

Pronotum with a shallow transverse indentation just anterior to the mid point. Mesonotum widens evenly from 3 mm to 6 mm at the hind margin. Metanotum and fused median segment of almost uniform width, widening only slightly at the point of insertion of the legs. Median segment slightly more than one third of the length of the metanotum.

Abdomen rugose and granulose throughout. Eleventh segment forms an almost equilateral triangle. Operculum granulate, with a deep keel and projecting beyond the end of the abdomen. Holotype without abdominal tubercles; paratype tuberculate, with lobe-like tubercles on the hind margin of segments 1, 2, 5, 7 and 8.

All femora with small spines or pointed lobes on the underside near the apices.

Base of fore femora constricted and inwardly curving. A slightly undulating foliaceous expansion forms a narrow lobe running along the upper surface of the femur. This lobe continues on the tibiae but is smooth, widening slightly at the apex. Fore tarsi missing from the holotype, those of the paratype have small lobes on the first three tarsomeres, decreasing in size towards the apex.

Mid femur thickened and bearing two lobes on the upper surface; a small rounded lobe near the base and a larger, pointed lobe two thirds of the way along (fig. 19). Mid tibiae with two lobes on the upper surface, one a third of the way along, and one at the apex. Tarsi short, not lobed.

Hind femora flattened. Tibiae with a small lobe on the underside at the base. Tarsi short, not lobed.

The male (figs. 3, 16, 22).— The end of the abdomen is missing from both males, one has clearly been damaged by insect pests, and has half of the head missing. The total length, given in tables 1 and 2, is taken from Günther's description (1943: 154); other measurements in table 2 are taken from the two paratypes. The general appearance is typical of many *Lonchodes* species (*L. amaurops*, *L. brevipes*, *L. jejunus*) but it may be distinguished from these by the back of the head which is conical in this species.

Body light brown with reddish brown patches at each end of the meso- and metathorax. The legs may have been greenish-brown originally with reddish-brown near the knees. Body, head, middle and front femora all densely granulose.

Table 2. Measurements of the new species. For the females of *P. nieuwenhuisi* only measurements of the holotype are given (* except for the fore tarsi which are missing from the holotype).

	<i>P. nieuwenhuisi</i> female	<i>P. nieuwenhuisi</i> males	<i>P. sepilokensis</i> females
Head and body	104	90	96-108
Antennae	>29	48	38-43
Head	4.5	3.5-4	6
Pronotum	4.5	2.5-3	4.5-5
Mesonotum	22	23-24	21.5-23
Metanotum	12	15	10.5-12
Median segment	6	4	4.5-5
Fore femora	18	20-21	18-20
Fore tibiae	16	19-22	18-20
Fore tarsi	4.5*	6	6.5
Mid femora	12	14.5-16	15-16
Mid tibiae	10	10-11	11.5-13
Mid tarsi	5	5	6
Hind femora	16	18-19	19-21
Hind tibiae	14.5	19-21	18.5-22
Hind tarsi	5.5	5.5	6.5

Head with two small spines between the eyes, back of the head conical (fig. 16). Antennae longer than the fore legs, of uniform thickness beyond the second segment. Basal segments slightly flattened, second segment almost as wide as long, first two segments about twice the width of the rest.

Pronotum with a transverse indentation at about the mid point. Thorax, and at least the first six abdominal segments, of uniform thickness except for thickening at the point of insertion of the legs. Median segment about one quarter of the length of the metanotum. Metanotum and median segment strongly arched upwards.

The end of the abdomen beyond the sixth segment is missing on both male specimens. Günther (1943: 154) described the end of the abdomen as having the last three segments decreasingly wide.

All femora armed with small spines on the underside near the apices. Upper surface of mid femora with an obvious pointed lobe on the upper surface close to the apices, four fifths of the way along (fig. 22). All tibiae without lobes. All tarsi short, without lobes, except for a small lobe on the first tarsomere of the fore tarsi.

The egg (figs. 6 & 7).— The egg is described from three of four eggs which were removed from the posterior portion of the abdomen of the holotype when it was relaxed and reset; the fourth egg was damaged during removal. Opercular angle about -6° .

Length 2.6-2.7 mm, height 1.9-2.0 mm, width 1.5-1.6 mm. Capsule and operculum light to mid brown. Surface uneven, composed of many fine, interlocking ridges, giving a general impression of being pitted. Micropylar plate cream, almost oval, narrowing at the opercular end. Micropyle at the polar end of the plate. A short median line runs one third of the way towards the polar mound. The polar mound, which is of variable size, has the appearance of a hollow, open ended cylinder which is split open on the dorsal side. Operculum almost circular, only slightly higher than

wide. There is a capitular stalk the length of which is indicative of a typical *Lonchodini* capitulum in a complete egg. During removal from the body, one egg had some material attached at the opercular end which may have been a capitulum.

The general appearance of the egg is very similar to several *Lonchodes* species (e.g. *brevipes* Gray, *jejunos* (Brunner), *amaurops* Westwood, and *haematomus* Westwood).

Distribution of the genus

The only reliable published records of *P. cornucervi* are from Mt Kinabalu in Sabah (East Malaysia). Günther (1932: 315) mentions a specimen of this species in the Berlin Museum marked "Labuan" but he seemed to have some doubt about this locality. The author has found this species to be quite common in the area around Mt Kinabalu Park Headquarters which is at an altitude of 1580 m. The BMNH has a number of specimens collected by Mr Allan Harman from this locality in the early 1980s. Mr C.L. Chan has collected it at this locality and also has in his collection a female specimen from Sinsuran in the Crocker Range, Sabah (personal communication, 1993).

The closely related *P. sepilokensis* is known from Sepilok Forest Reserve in Sabah (altitude c. 50 m), and a rather vague "Midden O-Borneo" [middle East-Borneo]. However large areas of eastern Borneo are below 500 m and most is below 1000 m, so it is quite likely that the specimens were collected from a lowland area.

P. verrucosus is recorded only from Batang Singalang in Sumatra (de Haan, 1842).

P. nieuwenhuisi is from Mahakam and Long Bloe-oe in Kalimantan (Günther, 1943). Mahakam refers to the River Mahakam and although attempts to locate Long Bloe-oe have been unsuccessful, it is assumed that this is also on the River Mahakam.

P. spinulosus has previously been recorded from two areas of Sabah, Sinsuran (Hausleithner, 1991) and near Mt Kinabalu Park Headquarters (Bragg, 1992a: 185). The author has found this species to be common along some of the trails in this area; in 1992, on three successive nights, three, one and nine adult specimens were counted. Mr C.L. Chan reports several specimens from these two localities (personal communication). In addition to several specimens from near Kinabalu Park Headquarters, the BMNH contains one specimen (BM 1964-25) which was collected at the Mesilau Camp of the Royal Society Expedition to Mt Kinabalu in 1964.

Rearing in captivity

Both *P. cornucervi* and *P. spinulosus* may be bred in a standard cage (Bragg 1989) at high humidity. Both species will readily feed on bramble (*Rubus* spp.), raspberry (*Rubus idaeus*), firethorn (*Pyracantha* spec.), dog rose (*Rosa canina*), ivy (*Hedera helix*), eucalyptus (*Eucalyptus gunnii*), oak (*Quercus* spec.) and flowering currant (*Ribes* spec.). The author has described the rearing of *P. spinulosus* in detail (Bragg, 1993) and rearing of *P. cornucervi* has been detailed by Raper (1987).

P. cornucervi has been observed to produce spermatophores (Bragg, 1992b). The eggs are dropped to the ground and take 5-7 months to hatch. Neither species is particularly difficult to culture; *P. cornucervi* is particularly easy if kept at a very high humidity and captive-reared livestock is available from commercial dealers in the UK.

Four eggs of *P. sepilokensis* were incubated and two hatched after 6 months. These

were maintained in a humid environment and fed on bramble, rose, oak, ivy, eucalyptus and firethorn. Both specimens lost legs during ecdysis, one specimen lost one hind leg, the other lost three legs and two of the remaining legs were slightly deformed. The specimen which lost three legs seemed unable to climb and lived on the floor of the cage, the other specimen underwent ecdysis several times while this remained at the same stage. When the damaged specimen lost a fourth leg it was killed and preserved. The other specimen developed into an adult female, laid 184 eggs, and died in April 1994. Just before it died, one egg laid by this specimen hatched, showing that the species is capable of facultative parthenogenesis. At the time of writing several eggs have hatched and some nymphs have reached the third instar; it seems probable that a sustainable culture will be established. If successfully reared, specimens reared from the paratype (PEB-2028) will be deposited at DCMD, NHMN, FRCS, and NHMW.

Phylogeny of the genus

In recent years the presence or absence of a capitulum on the egg has been used as an indicator of phylogenetic relationships, particularly by Sellick who concluded that "there is a general consistency within tribes" (1988: 297). In this genus, of the four for which the eggs are known, *P. cornucervi* and *P. sepilokensis* do not possess a typical Lonchodini capitulum, *P. spinulosus* clearly does, and *P. nieuwenhuisi* almost certainly does. At first sight this would suggest that the species are not closely related. However, the capitular structures of *P. cornucervi* and *P. sepilokensis* appear to be capitular stalks which are covered by the outer fibrous layer of the egg. The presence of a capitular stalk in the eggs of *P. cornucervi* and *P. sepilokensis* is evidence of a typical Lonchodini capitulum in the ancestral species. It seems likely that all members of the genus possessed a typical capitulum in the past, and these two represent species which have since lost the typical form. If this hypothesis is correct then Sellick's conclusion remains valid. These two species are very similar and probably diverged from a common ancestor, perhaps in response to altitudinal zonation.

Relationships between the other members of the genus are not so clear. The mid femoral lobes of *P. verrucosus* are similar in size and general shape to those of *P. cornucervi* and *P. spinulosus* while the back of the head is not truly conical and the lobes on the head are large, both features common to *P. spinulosus*.

The general appearances of both *P. nieuwenhuisi* and *P. spinulosus* are very similar to typical *Lonchodes* spp., as are their eggs. *P. spinulosus*, having a simple mid femoral lobe and lacking a conical bulge at the back of the head could be considered the closest to *Lonchodes*. Conversely, the general body proportions of both the males and females *P. nieuwenhuisi* are typical of *Lonchodes*; the mid femoral lobe of the female, although quite large, would not be exceptional for *Lonchodes*.

Phenacephorus (and also the related *Carausius* and *Lonchodes*) is perhaps a rather artificial taxon. One possible dendrogram is illustrated in figure 25, but a full phylogenetic analysis of this genus would be inappropriate at present for several reasons. The females of at least two of the species, *P. cornucervi* and *P. nieuwenhuisi*, are known to be quite variable and only one of the other species is recorded from more than one precise locality. Resolving the phylogeny of these groups would require more material than is currently available; specifically the male of *P. sepilokensis*, the male and egg

of *P. verrucosus*, and sufficient specimens to ensure that intraspecific variation does not affect the analysis. However, despite rather doubtful phylogenetic relationships, the combination of a lobed mid femur and obvious head ornamentation means that *Phenacephorus* remains a useful taxon for the purpose of identification.

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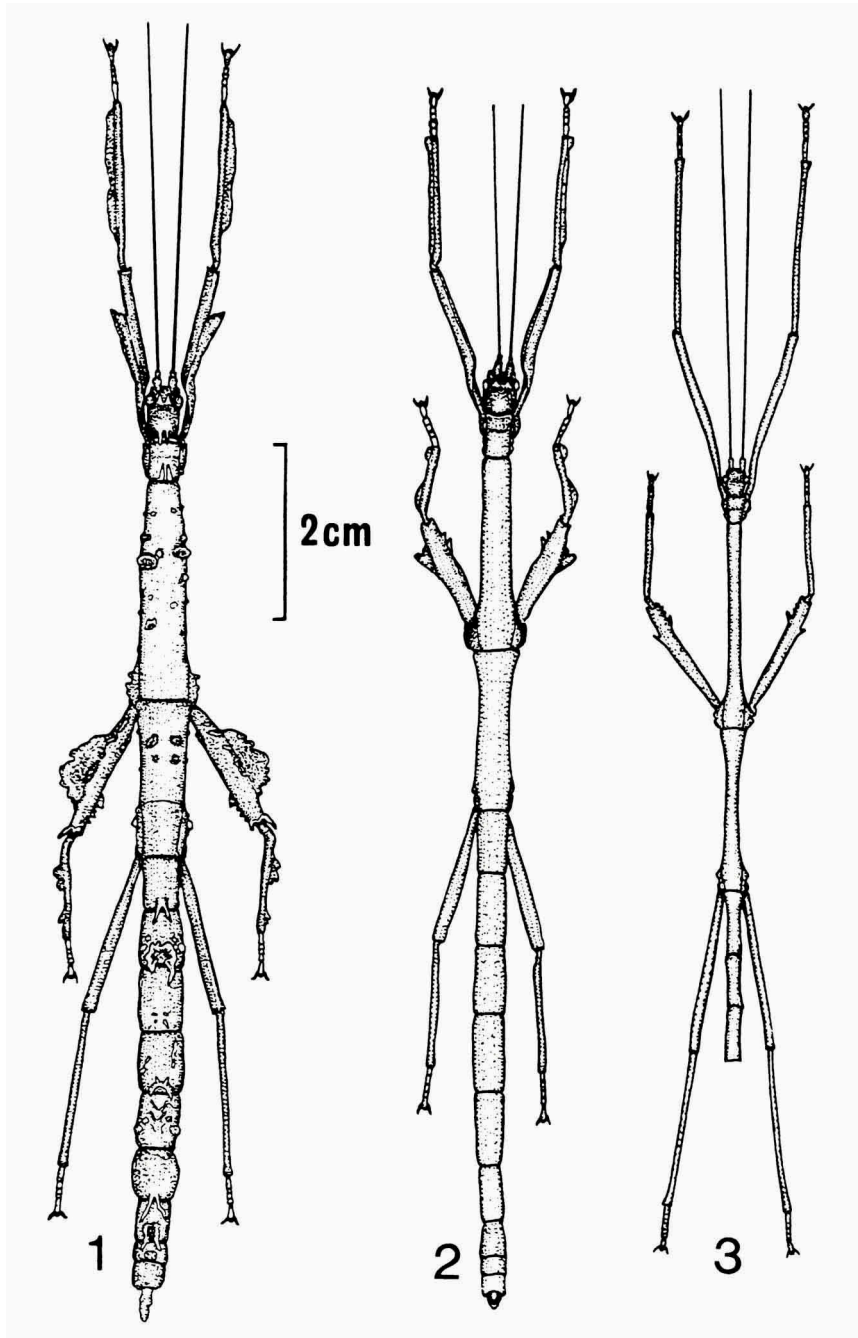
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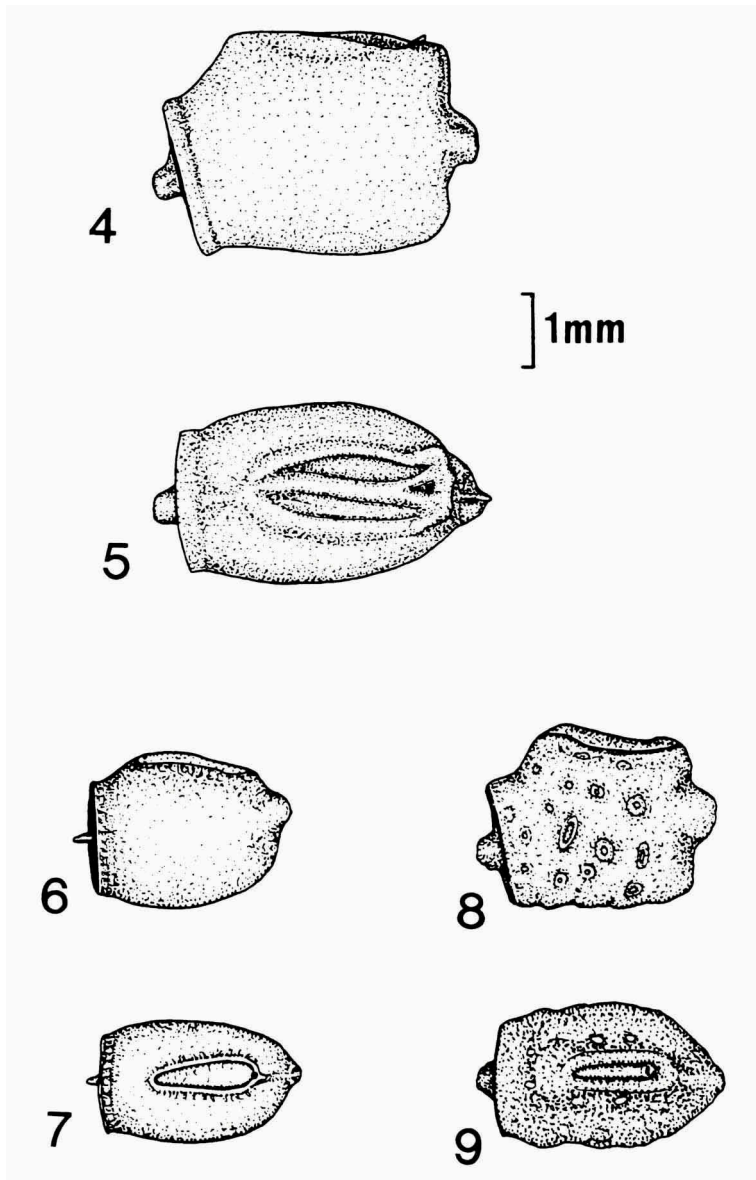
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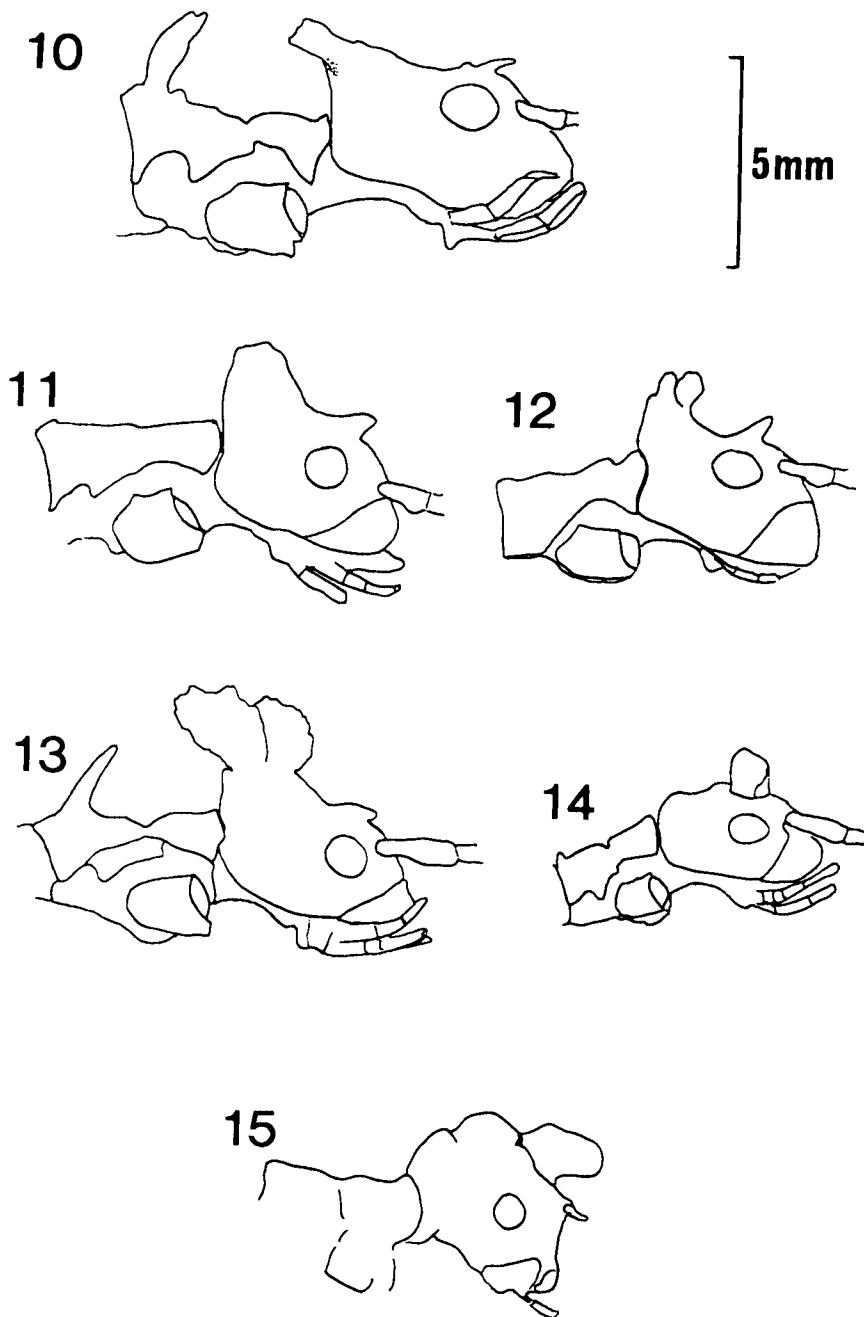
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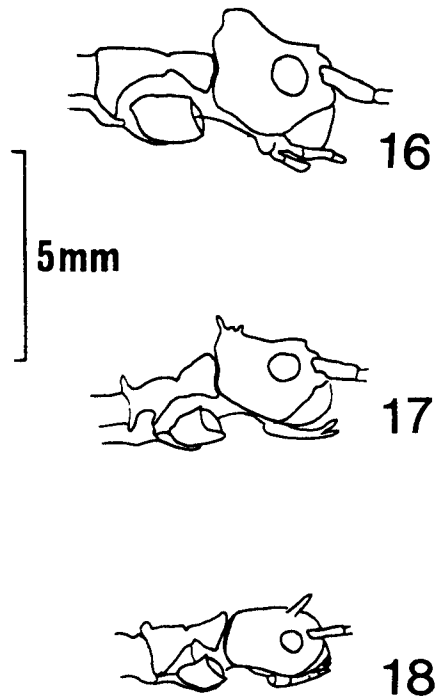
Figs. 1-3. 1, *P. sepilokensis*, ♀, holotype; 2, *P. nieuwenhuisi*, ♀, based on the holotype (missing fore tarsi added by reference to the paratype); 3, *P. nieuwenhuisi*, ♂.



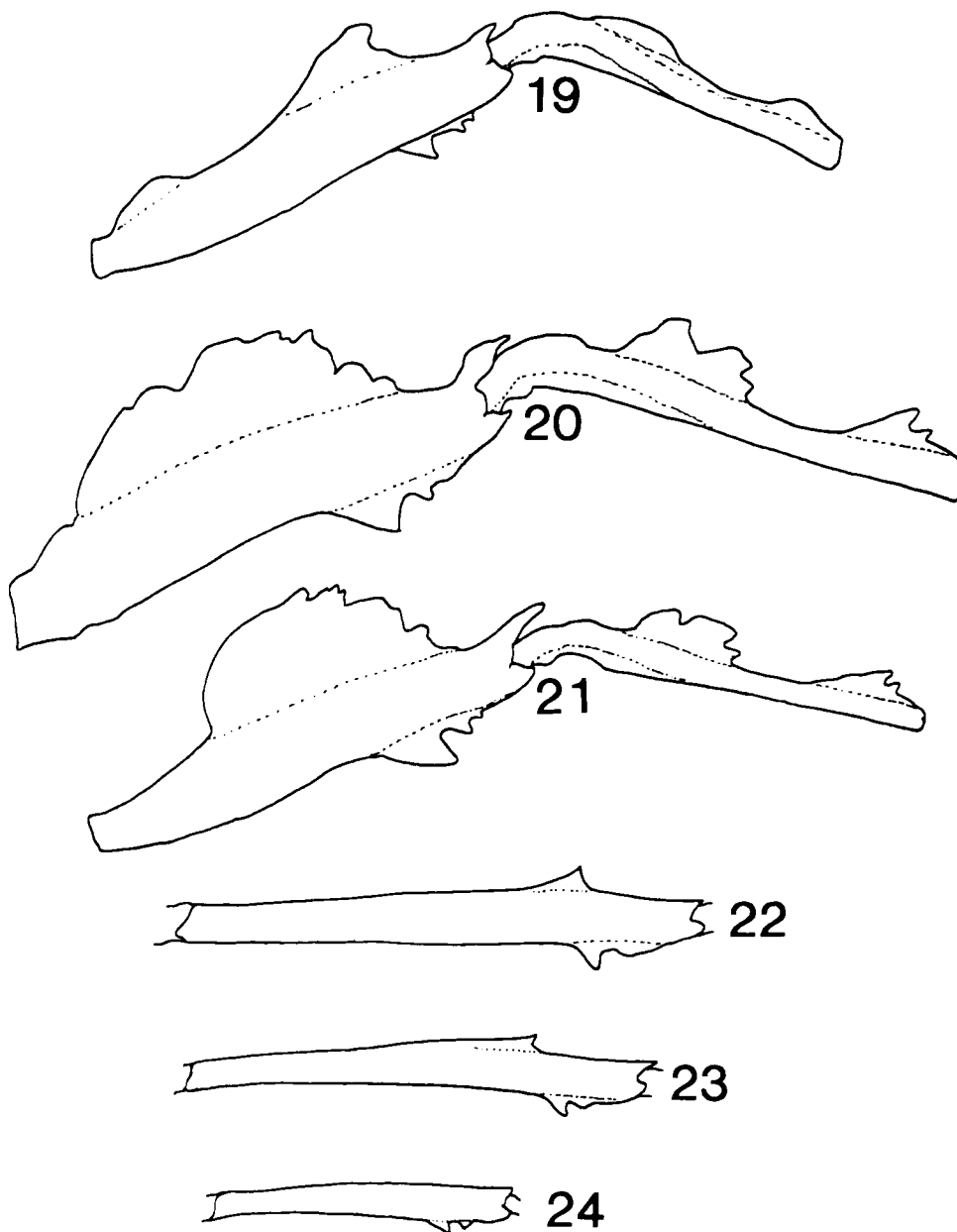
Figs. 4-9. Eggs: 4, lateral and 5, dorsal aspects of *P. sepilokensis*; 6, lateral, and 7, dorsal views of *P. niu-wenhuisi* (removed from holotype); 8, lateral, and 9, dorsal views of *P. cornucervi*.



Figs. 10-15. Lateral aspects of the heads of females: 10, *P. sepilokensis*; 11, *P. nieuwenhuisi*, holotype; 12, *P. nieuwenhuisi*, paratype; 13, *P. cornucervi*; 14, *P. spinulosus*; 15, *P. verrucosus* (from de Haan, 1842).



Figs. 16-18. Lateral aspects of the heads of males: 16, *P. nieuwenhuisi*; 17, *P. cornucervi*; 18, *P. spinulosus*.



Figs. 19-24. 19-21 Mid legs of females, 22-24 Mid femur of males: 19, *P. nieuwenhuisi*; 20, *P. sepilokensis*; 21, *P. cornucervi*; 22, *P. nieuwenhuisi*; 23, *P. cornucervi*; 24, *P. spinulosus*.

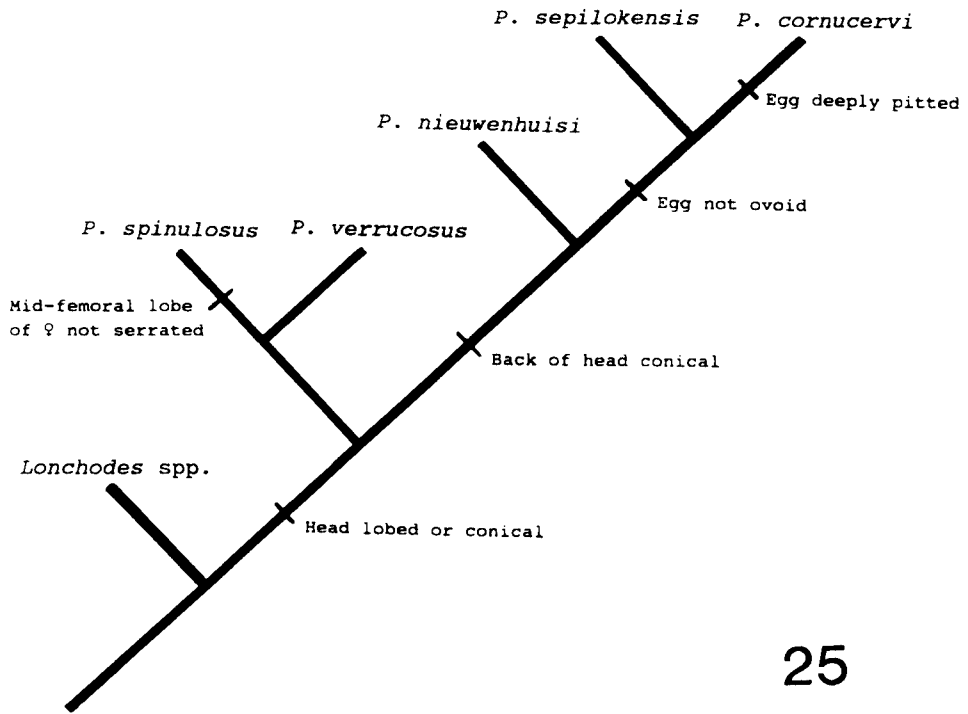


Fig. 25. A dendrogram representing a possible relationship between the species of *Phenacephorus*.