

ON THE SYSTEMATICS AND LIFE-CYCLE OF THE PENTASTOMID GENUS *KIRICEPHALUS* SAMBON, 1922 WITH DESCRIPTIONS OF THREE NEW SPECIES

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Summary

The three previously described *Kiricephalus* spp. are considered distinct because of differences in the number of abdominal annuli and differences in geographical and host distribution. Observations of a large number of specimens have confirmed the validity, and considerably extended the host list, of the two most common species, *K. pattoni* (Stephens, 1908), Sambon, 1922 and *K. coarctatus* (Diesing, 1850), Sambon, 1910. Generally annulus number is a satisfactory and reliable criterion upon which to separate species and three new species are described. One, *K. constrictor*, has an overlapping geographical distribution and annulus count with *K. coarctatus*, but comparative hook data reveals that they are unrelated. The life-cycles of the genus, reappraised in the light of the present findings, are shown to involve three vertebrate hosts. Eggs are only infective to amphibians, saurians or mammals, and snakes are second intermediate and definitive hosts, the final infection being acquired through ophiophagy.

Introduction

The three described *Kiricephalus* species are considered distinct because of differences in the number of abdominal annuli and of hosts and geographical distribution. Females are characterized by a globular cephalothorax separated from the abdomen by a neck-line constriction, an abdomen which is both twisted about its longitudinal axis and spirally coiled, and annuli

which are smooth and inconspicuous (Sambon, 1922; Fain, 1961). Males are less distinctive, notably lacking the neck, although the cephalothorax is still enlarged. Adults inhabit the lungs of snakes of the family Colubridae (Nicoli, 1963) but nymphs are less host-specific infecting amphibians, lizards, snakes and mammals (see Table I which summarizes the available information on hosts together with the references).

Of the two commonly encountered species, *K. coarctatus* (Diesing, 1850) Sambon, 1910, the type species of the genus, is widely distributed in North and Central American colubrids whereas *K. pattoni* (Stephens, 1908) Sambon 1922, occurs in Indian, South East Asian and Australian snakes and nymphal forms infect an unusually wide host spectrum (Table I). Hett (1924) recovered what she believed to be *K. pattoni* females from the lungs of a Madagascan snake, *Lioheterodon madagascariensis*, but they were so engorged by eggs that the number of annuli could not be estimated and this may be another species. Heymons (1935) recovered further specimens from a boa, *Corallus madagascariensis* but added nothing to its taxonomic status. Little is known of the remaining species *K. tortus* (Shiple, 1898) Sambon, 1922—the meagre type description is based on nymphs and mature females taken from *Boiga irregularis* in New Britain (Bismarck Archipelago, New Guinea) and it has since been recovered from this host in New Guinea (Ewers, 1973).

The published accounts of adult morphology are somewhat variable (Table II) mainly because they are based on observations of a few specimens, often from a single host (Sambon, 1910;

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Table I

The hosts of the three previously described species of *Kiricephalus*

Species	Definitive host	Source	'Intermediate' host	Source
<i>Kiricephalus coarctatus</i>	<i>Coluber constrictor constrictor</i>	Job & Cooper, 1917	<i>Micrurus fulvius</i> <i>Pituophis melanoleucus</i> <i>Mephitis mephitis</i>	Heymons, 1935
	<i>Masticophis flagellum</i> <i>Mastigodryas bifossatus</i> <i>Drymarchon corais couperi</i>	Heymons, 1935	<i>Lampropeltis getulus floridana</i>	Keegan, 1943
	<i>Chironius carinatus</i> <i>Lampropeltis getulus getulus</i> <i>Natrix fasciata fasciata</i> <i>Natrix cyclopion floridana</i> <i>Thamnophis sirtalis</i>	Hett, 1915 Keegan, 1943 Deakins, 1971		
	<i>Ptyas mucosus</i> <i>Ptyas korros</i> <i>Morelia spilotos</i>	Hett, 1921 Hett, 1924	<i>Bungarus fasciatus</i>	Hett, 1921
	<i>Xenochrophis piscator*</i> <i>Amphiesma stolata*</i>	Hett, 1934	<i>Felis domestica</i> <i>Xenochrophis piscator</i> <i>Amphiesma stolata</i> <i>Xenochrophis punctulatus</i>	Faust, 1927
	<i>Dendrelaphis calligaster</i>	Self & Kuntz, 1957	<i>Oligodon cruentatus</i> <i>Oligodon purpurascens</i> <i>Trimeresurus purpureomaculatus</i> <i>Bufo melanostictus</i> <i>Rana tigrina</i>	Hett, 1934
	<i>Elaphe carinata</i> <i>Zaocys dhumnades</i> <i>Elaphe taeniura</i> <i>Opheodrys major</i>	Self & Kuntz, 1960 Self & Kuntz, 1967 Keegan et al., 1969		
<i>Kiricephalus pattoni</i>			<i>Microhyla ornata</i> <i>Rana cancrivora</i> <i>Rana limnocharis</i> <i>Opheodrys major</i> <i>Trimeresurus mucrosquamatus</i> <i>Japalura swinhonis</i> <i>Bufo bankorensis</i>	Keegan, 1943 Self & Kuntz, 1967 Keegan et al., 1969
	<i>Boiga irregularis</i>	Shipley, 1898 Ewers, 1973	?	—

* doubtful—see the discussion.

Table II

The principal morphological characters of the three described species of *Kiricephalus* (from various authors)

Species	♀		♂		Source
	length mm	no. annuli	length mm	no. annuli	
<i>Kiricephalus pattoni</i>	80–115	36	?	?	Sambon, 1922
	120	?	25–37	33	Hett, 1924
	?	33–37	?	33–37	Hett, 1934
	105	?	55	?	Keegan et al., 1969
<i>Kiricephalus coarctatus</i>	?	50–52	?	?	Sambon, 1910
	50	50	?	?	Hett, 1915
	82–96	48–52(50)	14–30	48–52(50)	Job & Cooper, 1917
	76–115	indistinct	?	?	Sambon, 1922
<i>Kiricephalus tortus</i>	40	25	?	?	Shipley, 1898

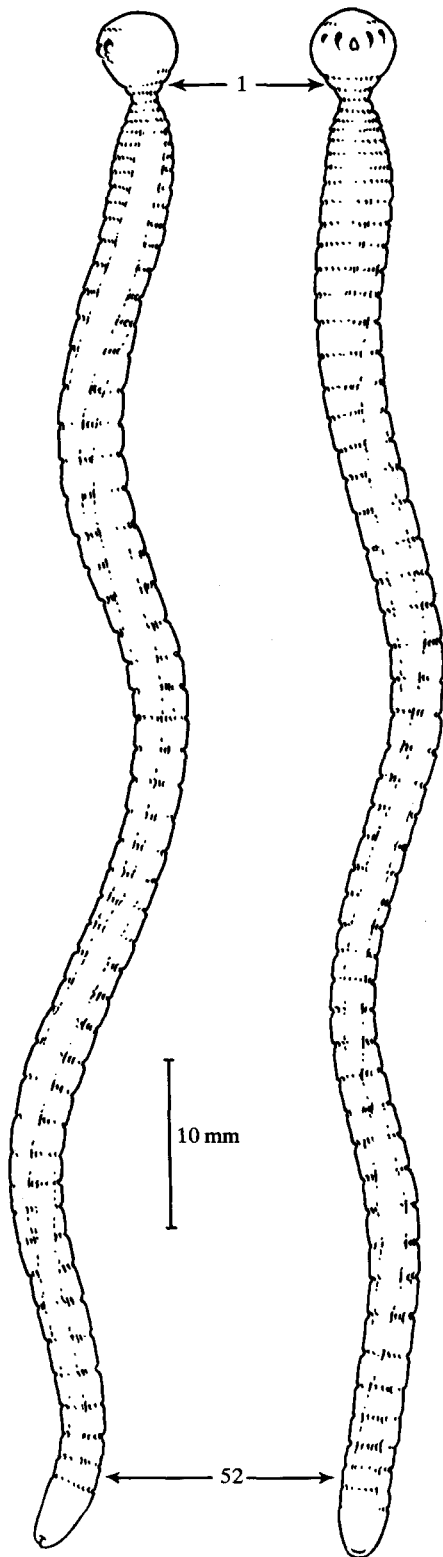


Fig. 1. A and B. Ventral and lateral aspects of a mature female of *K. coarctatus* (BM(NH) Reg. 1979.7.13.41-2) from *Drymarchon corais couperi*.

Hett, 1915, 1924, 1934; Heymons, 1935; Keegan, 1943; Keegan *et al.*, 1969) and virtually nothing is known of immature forms except for isolated accounts of nymphal *K. pattoni* (Faust, 1927; Hett, 1934; Keegan *et al.*, 1969).

The information presented in this paper summarizes observations of a large number of specimens taken from a variety of hosts. Modern descriptions of adult and nymphal *K. pattoni* and *K. coarctatus* are given and a more complete picture of the genus is provided by describing three new species. Additional information on host distribution and life-cycles is included.

Materials and methods

This study is based upon the collections of Dr. J. T. Self and the British Museum (Natural History) (Arachnid section): the former contains a large number of nymphal forms collected by Dr. R. E. Kuntz from autopsied reptiles captured on Taiwan and the Philippine Islands. Certain of the British Museum specimens, originally examined by Sambon, formed the basis of his taxonomic revision of the group (Sambon, 1922). The majority of the specimens were fixed and stored in 70% alcohol.

Counting the annuli

In order to obtain consistent and truly comparative data on the number of annuli we adopted the following counting procedure. In mature female specimens the globular cephalothorax carries two annuli with the second annulus usually forming the narrowest region of the neck (Figs. 2A, B, 4A, B). Each annulus carries a broad band of annular pits which mark the openings of the tegumental chloride cells (see Riley, James & Banaja, 1977) and these also serve as a guide to the number of annuli; this can be important in females distended with eggs. The terminal segment often carries rings of chloride cells but these are not delimited by annular depressions and are therefore included in the terminal segment (Figs. 1A, B and 3A, B).

Counting the annuli of males is straightforward: the prominent genital pore occupies the

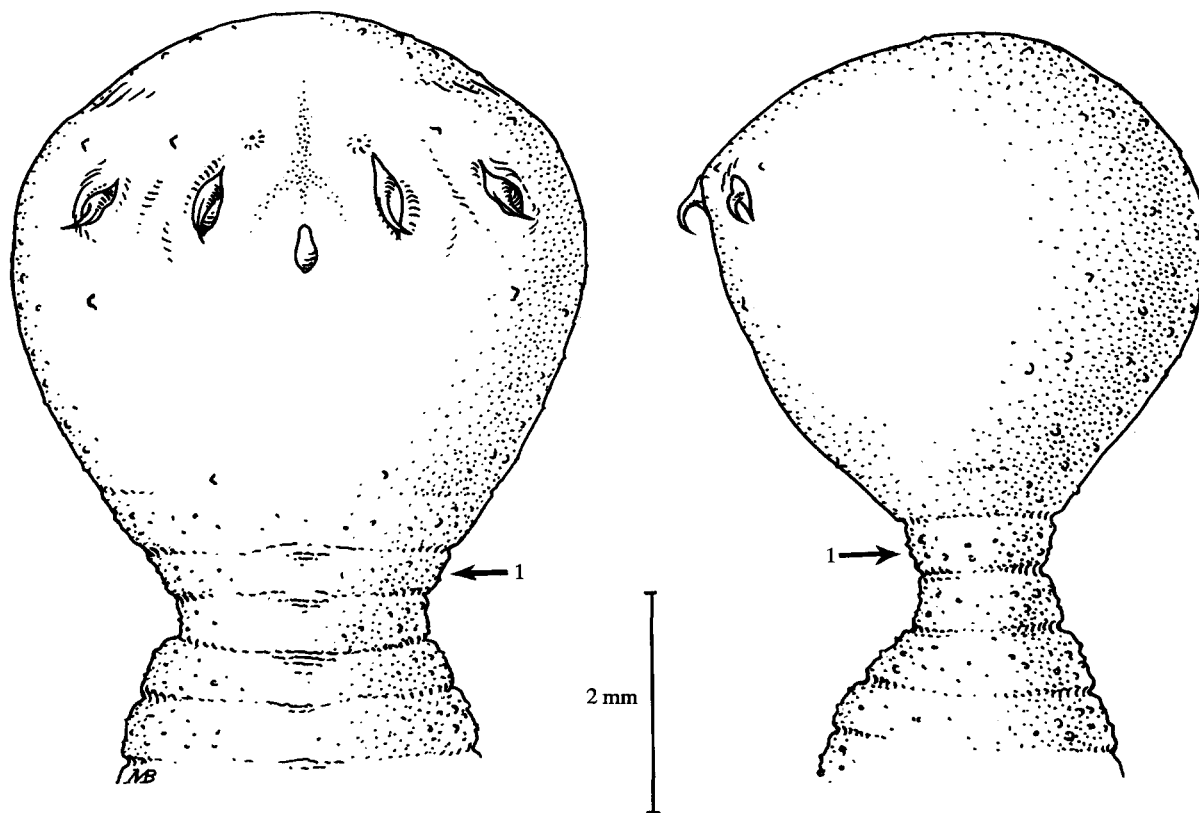


Fig. 2 A and B. Ventral and lateral aspects of the cephalothorax of a mature female of *K. coarctatus* (BM(NH) Ref. No. 1978.7.3.13.41-2)

first annulus (Figs. 3C, D) and the terminal segment is treated as above.

Hooks, dissected from specimens by fine needles, were dehydrated, cleared and mounted on slides and the over-all length (AD) was measured according to the convention of Fain (1961). This criterion was used to distinguish two sympatric species with overlapping annulus counts.

Results

General description (Figs. 1-4)

The cephalothorax of adult specimens is swollen, flattened ventrally, but rounded elsewhere. In mature females it is separated from the abdomen by a distinct neck formed by annuli II and III (Figs. 2A, B; 4A, B) and the abdomen is spirally coiled and twisted about its longitudinal axis

(Figs. 1A, B; 3A, B). In both sexes the pear-shaped mouth is positioned between the inner hooks which are consistently larger than the outer pair (Figs. 2A; 4A). The efferent ducts of the frontal glands erupt on to the cuticle through paired frontal papillae which are located above the mouth and between the inner hooks. Four pairs of small sensory papillae occur on the ventral cephalothorax (Figs. 2A; 4A): the three most anterior pairs occupy similar positions in both sexes but the remaining pair of the female lie at the lower edge of the cephalothorax (Figs. 2A; 4A) whereas those of the male flank the genital pore on annulus I. Males are claviform and taper gradually towards the caudal extremity (Fig. 3C, D). The crescentic common opening of the vagina and anus of the female is ventral and subterminal in position as is the anus of the male.

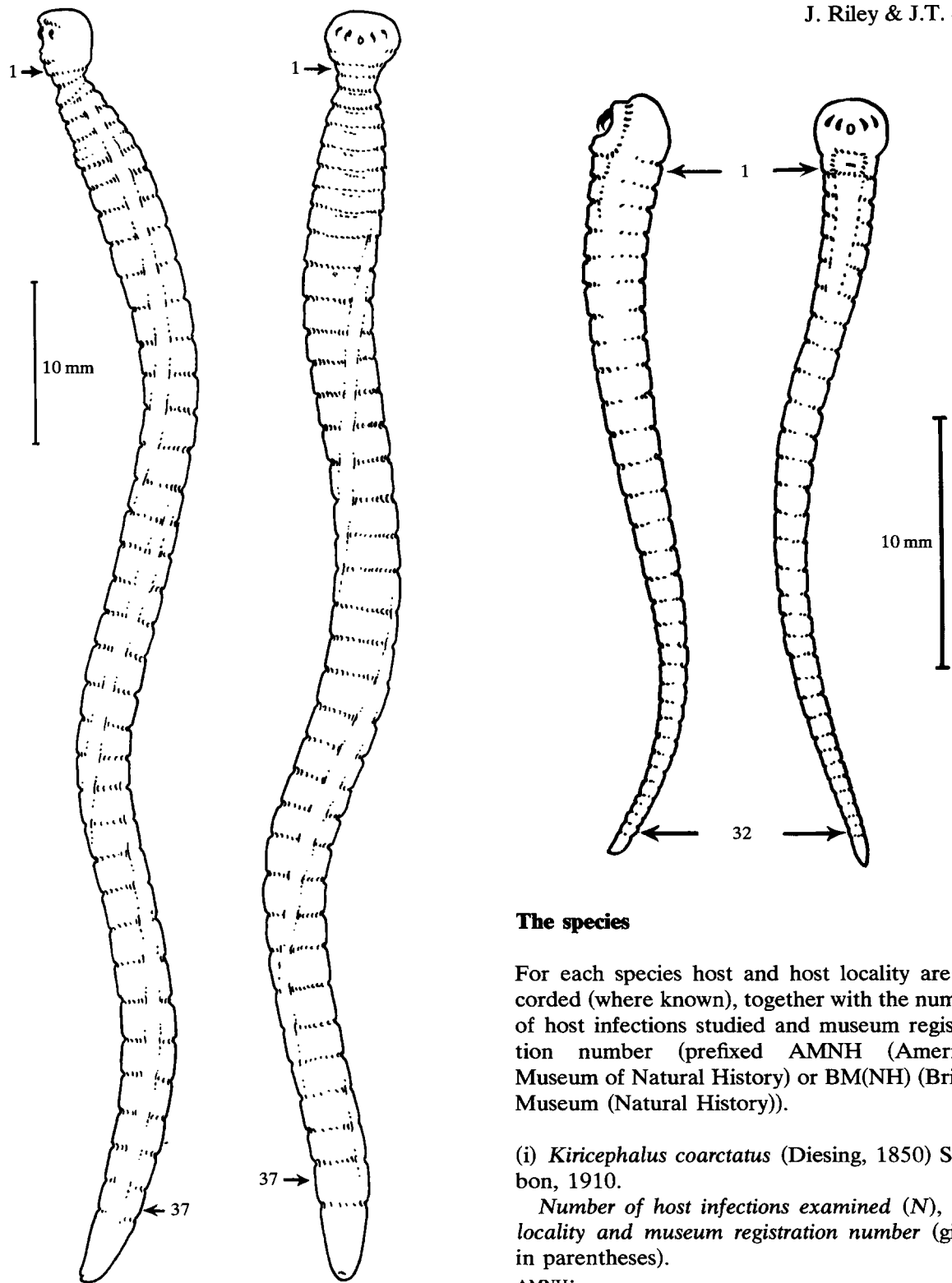


Fig. 3 A and B. Ventral and lateral aspects of a mature female of *K. pattoni* (BM(NH) Ref. No. 1978.7.13.56-59) from *Ptyas mucosus*. C and D. Ventral and lateral aspects of a male (BM(NH) Ref. No. 1978.7.13.45-51).

The species

For each species host and host locality are recorded (where known), together with the number of host infections studied and museum registration number (prefixed AMNH (American Museum of Natural History) or BM(NH) (British Museum (Natural History))).

(i) *Kiricephalus coarctatus* (Diesing, 1850) Sambon, 1910.

Number of host infections examined (*N*), host locality and museum registration number (given in parentheses).

AMNH:

Adults in : *Drymarchon corais couperi* (*N* = 22), Texas, Florida and various zoos, (148, 151-2, 154-5, 157, 161, 166, 254-6, 285-6); *Elaphe*

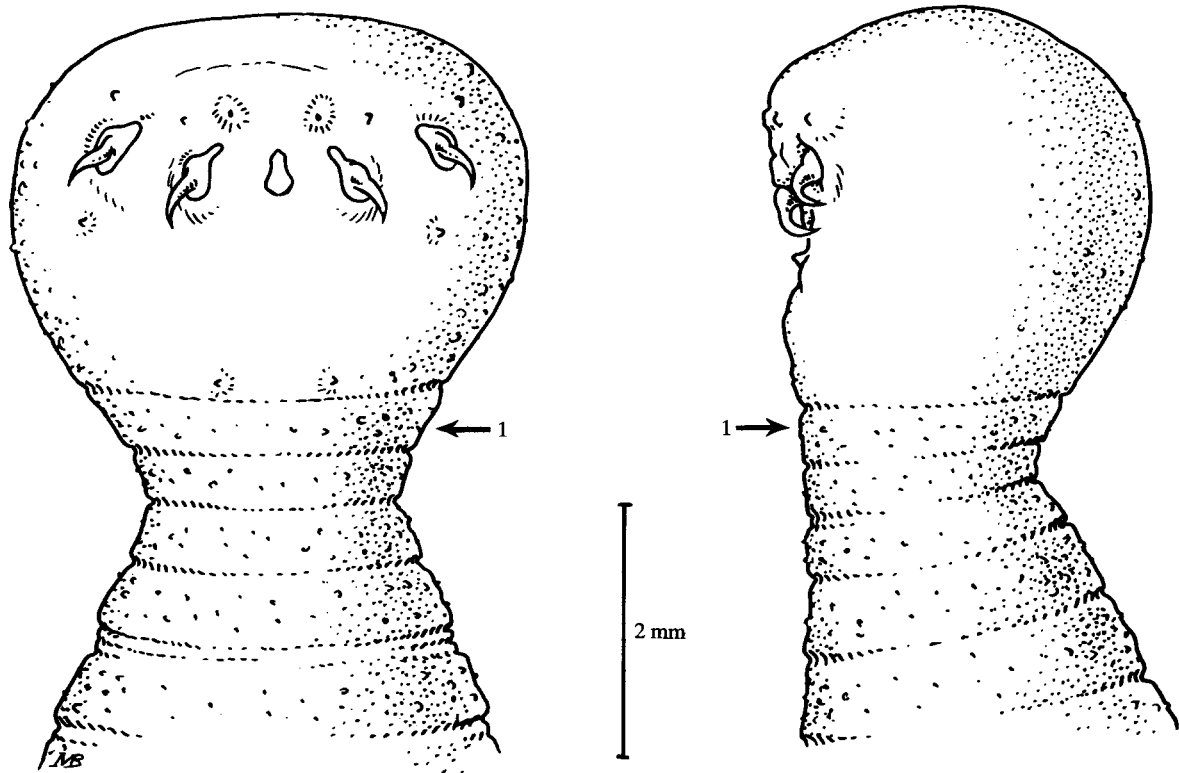


Fig. 4. Ventral and lateral aspects of *K. pattoni* showing detail of the cephalothorax (BM(NH) Ref. No. 1978.7.13.56-69).

*obsoleta** (N=1), ?, (156); *Masticophis flagellum* (N=1), Minnesota, (236).

Nymphs in: *Coluber constrictor foxii** (N=1), Dakota, (235); *Erythrolamprus bizona** (N=1), Panama, (283); *Lampropeltis getulus getulus* (N=1), Fla., (165); *Natrix cylopion* (N=1), La., (149); *N. erythrogaster transversa** (N=2), ?, (162); *N. fasciata fasciata* (N=2), Fla., (168); *N. rhombifera** (N=1), ?, (158); *N. sipedon sipedon** (N=2), ?, (163); *N. taxispilota** (N=2), Ga., and ?, (153, 160); *Natrix* sp. (N=1), ?, (164); *Pituophis melanoleucus* (N=1), Fla., (167).

BM(NH):

Adults in: *Drymarchon corais couperi* (N=6), Fla., (1927) II. 15.62-68, 1978.7.13.1-10, 1978.7.13.31-42); *Lampropeltis getulus getulus* (N=1), ?, (1927 II 15.31); *Natrix erythrogaster** (N=1), Texas, (1978.7.13.17-20); *Natrix*

sp. (N=1), N. America (1978.7.13.21-23).

Nymphs in: *Agkistrodon piscivorus** (N=1), ?, (1978.7.13.43-44); *Crotalus adamanteus** (N=1), Fla., (1978.7.13.11-16); *Erythrolamprus aesculapii** (N=1), Bolivia (1932.12.1.49); *Thamnophis sirtalis** (N=1), ?, (1978.7.13.24-30).

Systematic description (Figs. 1A, B; 2A, B)

Mature females: (N=20), 81-114 mm long (\bar{x} = 89), annuli 49 to 53 (\bar{x} = 51). Diameter of cephalothorax 4.5-5.0 mm, neck 2.0-2.5 mm, and abdomen 2.5-3.0 mm.

Maturing females: (from *D. corais couperi* and *N. erythrogaster*) (N=11), 44-56 mm long with 47 to 55 annuli (\bar{x} = 51).

Mature males: (all dissected), (N=3), 30-35 mm long (\bar{x} = 33), 50 annuli.

Infective nymphs: Females (N=19), 20-24 mm long (\bar{x} = 22), 47 to 55 annuli (\bar{x} = 51).

Males (N=5) 18.0-21.5 mm long (\bar{x} = 20), 46 to 48 annuli (\bar{x} = 47).

* Indicates new host record.

Immature nymphs 8–16 mm long possess 48 to 49 annuli.

(ii) *Kiricephalus pattoni* (Stephens, 1908) Sambon, 1922.

Number of host infections examined (N) and museum registration number (given in parentheses). All specimens from Taiwan except where otherwise indicated.

AMHN:

Adults in: *Elaphe carinata* (N=5), (56–58); *Ptyas mucosus* (N=55), (103–115, 122–3, 131–2, 134–6, 138, 257–8, 260); *Ptyas korros* (N=13), (82–88); *Zaocys dhumnades* (N=13), (89–93).

Nymphs in: **Ophidia:** *Agkistrodon acutus** (N=2), (39, 118); *Boiga kraepelini** (N=3), (50–1) *Bungarus multicinctus* (N=2), (65, 121); *Elaphe porphyracea** (N=2), (41, 119); *Enhydrys chinensis** (N=1), (45); *E. plumbea** (N=2), (44, 64); *Dinodon rufuzonatum** (N=10), (70–3); *Opheodrys major* (N=18), (94–5); *Naja naja** (N=2), (40, 59); *Naja** sp., (N=1), South India, (133); *Natrix annularis** (N=2), (46–7); *Xenochrophis piscator* (N=11), India and Taiwan, (78–81, 273); *Amphiesma sauteri** (N=1), (37); *A. stolata* (N=9), (74–77); *Natrix percarinata suriki** (N=1), (42); *Rhabdophis swinhonis** (N=1), (43); *Psammodynastes pulverulentus** (N=2), (48–9); *Morelia spilotos* (N=1), ?, (128); *Trimeresurus gramineus** (N=2), (117); *T. mucrosquamatus* (N=15), (96–100, 125–7, 259); *T. stejnegeri** (N=5), (54–5, 66, 116); *Vipera russelii** (N=5), (52–3, 124).

Lacertilia: *Hemidactylus frenatus* (N=1), (61); *Japalura swinhonis* (N=1), (62).

Amphibia: *Bufo bufo* (N=2), (38, 60); *B. melanostictus* (N=2), (36, 63); *Rana limnocharis** (N=3), (68); *Rana* sp. (N=1), (67).

BMNH:

Adults in: *Ptyas mucosus* (N=9), India, S.E. Asia, Java, Taiwan, (1922.7.15.1–9; 1927.2.15.09; 1927.2.15.70–71; 1947.12.1.62; 1948.8.6.2–4; 1978.7.13.45–59); *Elaphe carinata* (N=1), (1978.7.13.100–102); unknown hosts, (N=2), (1932.6.22.8 & 9); *Chrysopodea ornata**, (N=1), Indo-China, (1979.1.10.22–24); *Calliophis bibroni**, ?, (1979.1.10.40).

Nymphs in: *Opheodrys major* (N=1),

(1978.7.13.60–73); *Natrix* sp., (1978.7.13.99); *Plectrurus perroteli** (N=1), ?, (38); *Trimeresurus mucrosquamatus* (N=1), (1979.1.10.5.21); *Vipera ammodytes** (N=1), West Asia (?), (1978.7.13.74–98); unknown host, Hong Kong, (1927 III.10.21–26).

Amphibia: *Bufo melanostictus*, (N=1), Hong Kong, (1979. 10.1.3–4).

Systematic description (Figs. 3A, B, C, D; 4A, B)

Mature females: (N=17), 83–137 mm long (\bar{x} = 100), annuli 34 to 38 (\bar{x} = 36.5). Diameters of cephalothorax and abdomen 4 mm, neck 2 mm.

Mature males: (N=2), 28 and 29 mm long with 31 and 32 annuli respectively.

Infective nymphs: females: (N=33), 11–22 mm long (\bar{x} = 15), annuli 34 to 38 (\bar{x} = 36.5).

Males: (N=15), 9–18 mm long (\bar{x} = 13), annuli 31–35 (\bar{x} = 33). (Fig. 9A–D).

Smallest nymphs: from *Vipera ammodytes* (N=4), 4–5 mm long, 31 to 33 annuli.

(iii) *Kiricephalus clelii* n.sp. (Fig. 5A, B, C, & D).

Diagnosis based on six immature individuals (4♀, 2♂) recovered from two specimens of the pseudoboa (*Clelia clelia*) taken on the Island of Trinidad, West Indies.

Systematic description (Fig. 5).

Female: Holotype (AMNH 332) 48 mm long with 47 to 48 annuli. (Fig. 5A, B). Paratypes (AMNH 332 A and 329) 54, 46, 22 mm long with 46, 47 and 48 annuli respectively.

Males: Paratype (AMNH 332) 19 mm long with 38 annuli. (Fig. 5C, D).

Paratype (AMNH 329) 16 mm long with 42 annuli.

(iv) *Kiricephalus constrictor* n.sp. (Fig. 6A, B).

Diagnosis based on an immature male and female taken from the lungs of an autopsied boa (*Boa constrictor*) at Chicago Zoo.

Systematic description

Paratype female (BMNH 1979.1.10.1–2): 16 mm long with 54 annuli Holotype male

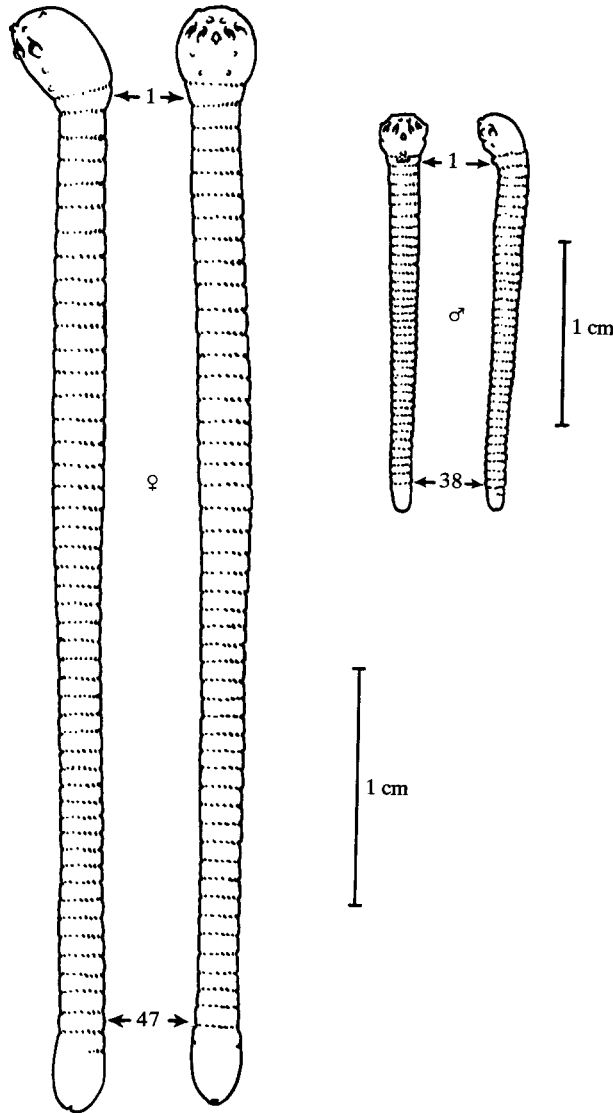


Fig. 5. A, D. Ventral and lateral aspects of the holotype female and paratype male of *K. clelii* n.sp. (AMNH 332).

(BMNH 1979.1.10.1-2): 25 mm long with 54 annuli. (Fig. 6A, B).

(v) *Kiricephalus gabonensis* n.sp. (Fig. 7A, B).

Diagnosis based on two immature females recovered from *Miodon gabonensis* taken at Metet, French Cameroon, Africa.

Holotype (AMNH 140): 36 mm long with 74 annuli

Paratype (AMNH 140A): 31 mm long with 75 to 76 annuli.

The taxonomic status of the remaining three 'species' of *Kiricephalus* is uncertain because all are infective nymphs (see the discussion).

(vi) *Kiricephalus* sp. from *Bothrops atrox*. (Fig. 8A, B, C & D).

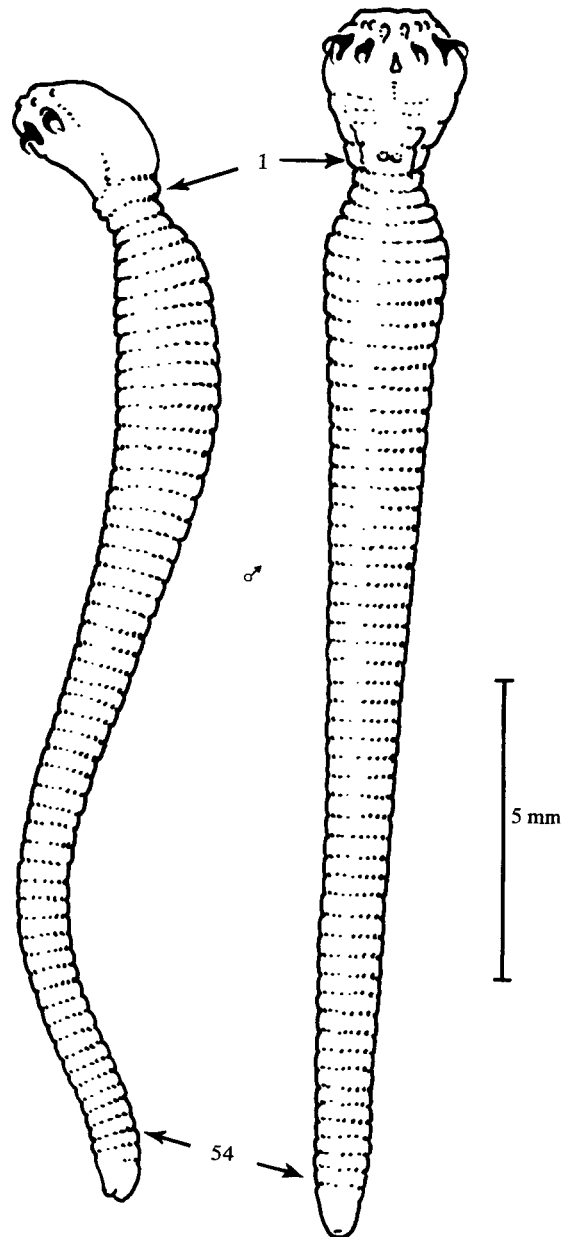


Fig. 6. A and B. Ventral and lateral aspects of the holotype male of *K. constrictor* n.sp. (BM(NH). Ref. No. 1979.1.10.1-2).

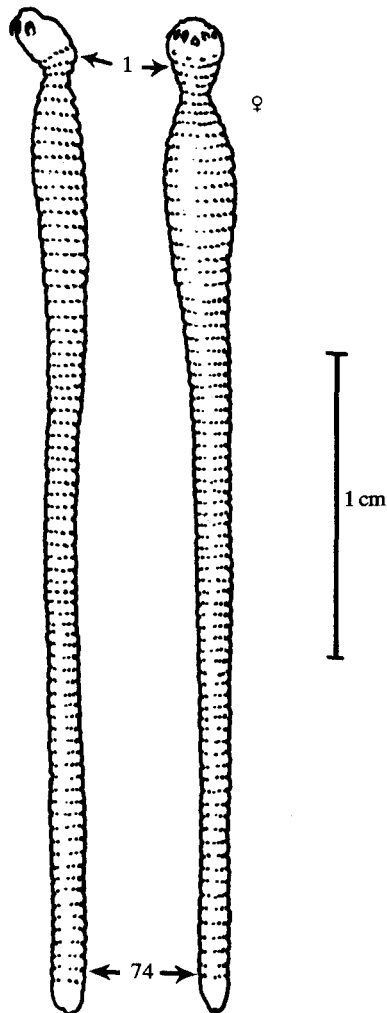


Fig. 7. A and B. Ventral and lateral aspects of the holotype female of *K. gabonensis* n.sp. (AMNH 140)

Diagnosis based on 12 nymphs (AMNH 331) recovered from a Fer-de-lance (*Bothrops atrox*) from the Island of Trinidad, West Indies.

Females: (N = 6), 16–19 mm long (\bar{x} = 17), 44 to 45 annuli.

Males: (N = 6), 13–15 mm long (\bar{x} = 14), 40 to 43 annuli (\bar{x} = 42).

(vii) *Kiricephalus* sp. from *Drymobius boddaerti*

A single male nymph (BM(NH) 1927 XII. 23.2–3) from Gorgona Island, Colombia: 8 mm long, 31 annuli.

(viii) *Kiricephalus* sp. (host unknown)

Six specimens (BM(NH) 1926.1.27.606–611) from Gorgona Island, Colombia.

Females: (N = 4) 14–15 mm long, 41 to 42 annuli

Males: (N = 2) 11 and 12 mm long, 37 or 38 annuli.

Comparison of the hooks of K. coarctatus, K. pattoni and K. constrictor n.sp.

The inner hooks of all the *Kiricephalus* spp. examined were bigger than the outer pair; the measurement AD (the over-all hooklength) revealed a consistent difference of about 10%. Only inner hook measurements are used in Fig. 10.

Preliminary observations indicated that body length was not well correlated with hook size probably because of inconsistencies in fixation combined with allometric growth. The nature of the relationships between these two parameters for females of *K. coarctatus* and *K. pattoni* (the only species for which all stages from infective nymph to mature adult were available) is shown in graphical form (Fig. 10). The two species display different growth characteristics and, in both, the latter stages of growth, which we assume involves periodic ecdysis, do not involve a concomitant increase in hook size. When values for a male and female *K. constrictor* n.sp. (which has a similar annulus number and distribution to *K. coarctatus*) are compared, it is clear that the two species are unrelated (Fig. 10).

Data from dissected males of *K. coarctatus* and *K. pattoni* are included to reinforce the point. The other species are separable by other criteria (see the discussion).

Discussion

Some justification of the new species is appropriate since all were immature and in certain porocephalid genera, for example *Porocephalus*, annulus number alone is an inadequate criterion upon which to separate species (Riley & Self, 1979). Self (1969), observed that the number of annuli is variable and is probably not consistent until after the last moult. However, the present

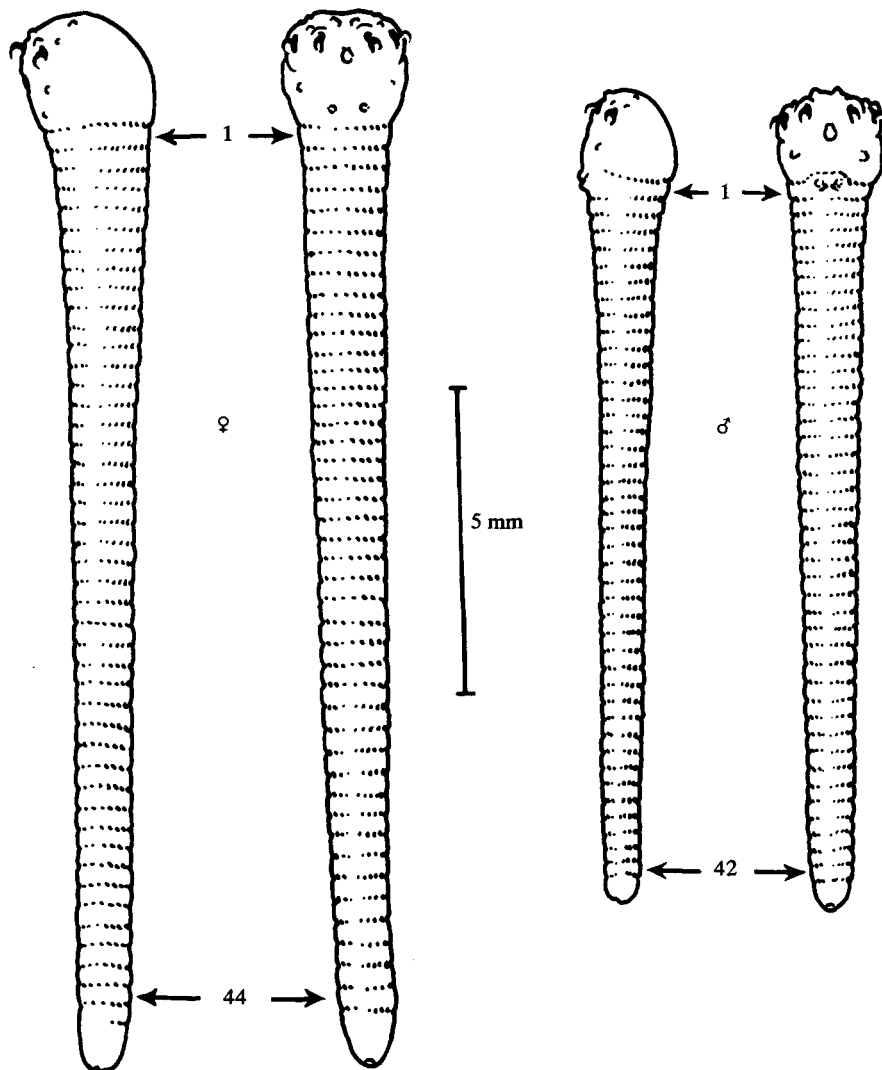


Fig. 8. A-D. Ventral and lateral aspects of a male and female of *Kiricephalus* sp. from *Bothrops atrox* (AMNH 331).

observations of comparatively large numbers of both adult and nymphal *K. pattoni* and *K. coarctatus* indicate that within this particular genus there is much less difference than was previously supposed and that these two species can be readily differentiated using this sole criterion. There is every reason to assume that this applies to the other species and therefore *K. clelii* n.sp. and *K. gabonensis* n.sp. are immediately distinguished. However annulus number of *K. constrictor* overlaps with that of *K. coarctatus* as does the geographical range, but by plotting mean inner hook length against body

length it is clear that the two are unrelated (Fig. 10).

The three 'species' comprising infective nymphs from South American snakes are probably all new species since their annulus counts differ from each other and from the other sympatric species. All three infections probably involve the second intermediate host (see below).

We have had no opportunity to examine specimens of *K. tortus* but the type description (Shiple, 1898, 1900), though perfunctory, leaves little doubt as to its validity: mature females are 40 mm long with approximately 25 annuli.

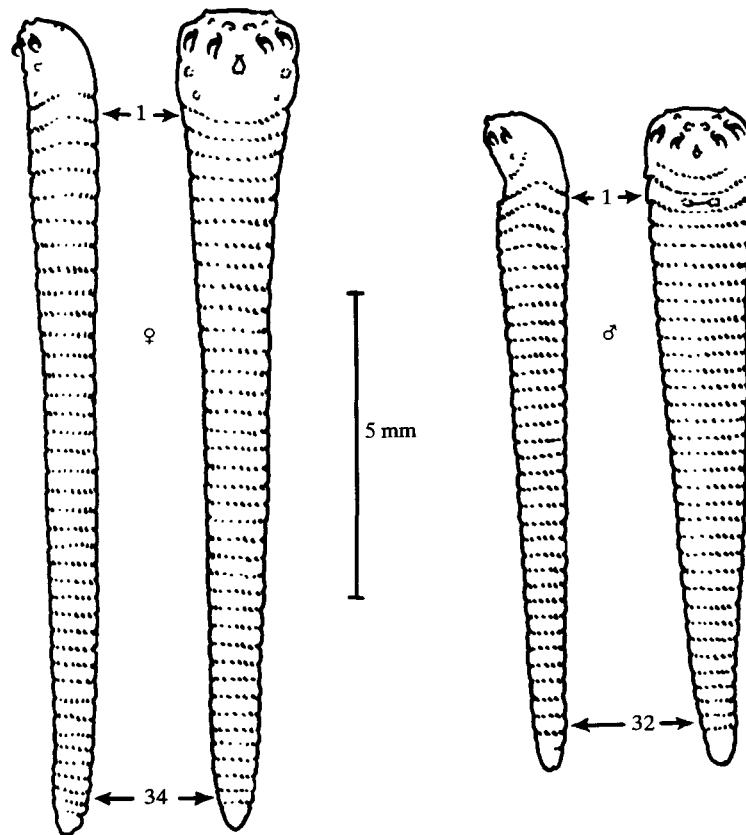


Fig. 9. A-D. Ventral and lateral aspects of male and female infective nymphs of *K. pattoni* (BM(NH) Reg. No. 1979.1.10.5.21) from *Trimeresurus mucrosquamatus*.

K. coarctatus and *K. pattoni* infect an impressive number of snakes, lizards, amphibians and mammals and this will probably prove to be the case with many of the other species as more information becomes available. The roles of many of the hosts in the life-cycle of *Kiricephalus*, at present unknown, can be reassessed in the light of this paper.

For example, in the case of *K. pattoni*, our observations and those of Prasad (personal communication) cast considerable doubt upon the claims of Hett (1934) that *Natrix* sp. are utilized as definitive hosts. Prasad dissected 100 *Ptyas mucosus* and 680 *Xenocrophis piscator* collected from the same locality. Nymphal infections, extremely common in *Xenocrophis*, were confined to the body-cavity, whereas in *Ptyas*, only adults were found and these exclusively in the lung.

Likewise Self & Kuntz (1967), from observations of a variety of naturally infected snakes

noted that in definitive hosts, notably *P. mucosus* and *Zaocys dhumnades* the heads of adult worms were usually buried deep in the lung

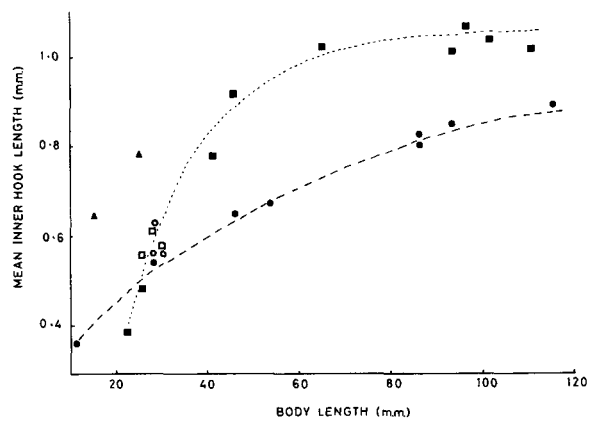


Fig. 10. Plots of mean inner hook length (AD) against body length of *K. coarctatus* (■), *K. pattoni* (●) and *K. constrictor* n.sp. (▲). (Solid symbols = ♀; open symbols = ♂).

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lining and only very occasionally were they elsewhere, on the pleura and viscera. By contrast, in two obviously intermediate hosts, *Opheodryas* (= *Liopeltis*) *major* and *Trimeresurus mucrosquamatus* extensive nymphal infections were exclusively visceral. Keegan *et al.* (1969) also recorded adults from *O. major* but we consider this unlikely since we examined 18 infections, each usually comprising at least 10 worms, and all were nymphs. It is perhaps worth emphasizing at this point that the nymphs from snake 'intermediate hosts' are never larger than 22 mm in the case of *K. pattoni* (Fig. 9) and 24 mm long in the case of *K. coarctatus*, whereas those from definitive hosts are rarely less than 40 mm long.

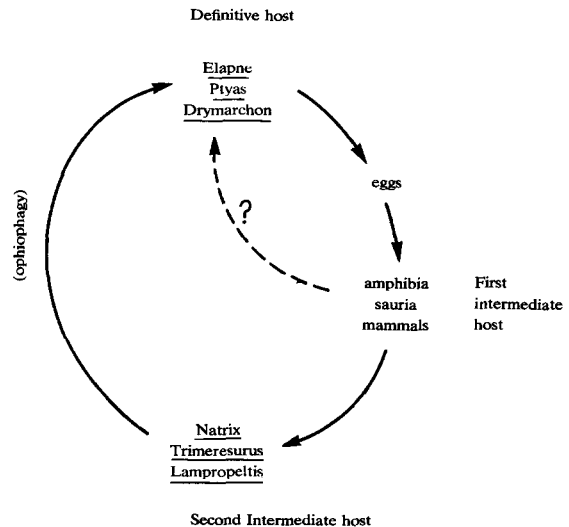
A number of experimental investigations into the life-cycle of *K. pattoni* have yielded some interesting results. Salazar (1965) gave eggs to a wide variety of experimental hosts (unspecified) but failed to establish an infection, whereas nymphs fed to frogs and toads survived for several months, indicating a paratenic or transport role for these hosts. Keegan *et al.* (1969) fed eggs to an agamid lizard (*Japalura swinhonis*) and a toad (*Bufo bankorensis*) and recovered encysted nymphs at autopsy 90 days later. These observations were qualified by the statement "that since both hosts had been captured as adults on Taiwan, there was no assurance that these collections represented experimental infections". Some unpublished results of Deakins & Self vindicate these results because laboratory stocks of *Rana pipiens* and *Bufo woodhousei* given eggs of *K. pattoni* per os yielded nymphs from the liver, lungs and viscera.

Clearly both reptiles and amphibians are involved in the life-cycle of *Kiricephalus* spp. The crucial experiments of Keegan (1943), on the life-cycle of *K. coarctatus*, now enable us to ascribe precise roles to each. Keegan discounted the possibility of a direct life-cycle because eggs, shed by gravid females into water, failed to infect three snake species known to be definitive hosts. But significantly, eggs also failed to infect *Elaphe* (= *Pituophis*) *melanoleucus*, a known intermediate host (Table I).

In summary: (a) amphibians and lizards and, probably, mammals (Table I) can be directly

infected by *Kiricephalus* eggs and are therefore, first intermediate hosts: (b) many species of snakes act as second intermediate hosts because they carry extensive nymphal infections and yet are refractory to infection with eggs; and (c) most of the definitive hosts have catholic diets which commonly include mammals, other reptiles and/or amphibians (Table III).

The life-cycle can be diagrammatically represented thus:



This is the first pentastomid life-cycle known to involve three hosts. As yet there is no good evidence to suggest whether or not the snake second intermediate host is obligatory but the common occurrence of such naturally infected hosts indicate that this is likely. However snakes are absent from the diets of certain definitive hosts (Table III) but since there is only a limited amount of information available on this subject these might well be consumed in the wild. The assertions of Hett (1924), Self & Kuntz (1967) and Self (1969) that direct development in *Kiricephalus* is possible because both nymphs and adult worms occur in snakes, are therefore, mistaken.

Self & Kuntz (1967) observed that when snakes harbouring nymphal infections are stressed, by either rough handling or drowning, the nymphs are stimulated into active migration and often crawl out of the host through rents in the

Table III

The principal prey of selected snake species harbouring nymphal and adult *Kiricephalus* spp. (information supplied by D. Ball, Overseer of Reptiles (London Zoo)).

Species	Prey
<i>Drymarchon corais couperi</i>	Small mammals, birds and snakes
<i>Masticophis flagellum</i>	Mammals, small birds, snakes occasionally
<i>Elaphe carinata</i>	Small snakes and rodents
<i>Ptyas mucosus</i>	mainly mammals and birds, also snakes
<i>Zoacys dhumnades</i>	Amphibians and rodents
<i>Boiga irregularis</i>	Lizards, small birds and mammals
<i>Natrix sipedon</i>	mainly fish and amphibians
<i>Natrix cyclopion</i>	fish, frogs and salamanders
<i>Ophedryas major</i>	small rodents
<i>Morelia spilotos</i>	mammals and birds

epidermis or through the mouth and nares. Although no explanations of these singular phenomena were advanced at the time, probably because the distinction between definitive and second intermediate host was not realized, it is now apparent that the escape response was initiated on the expectation that the nymphs would emerge into the stomach of an ophiophagous definitive host. Similarly, if mice harbouring encapsulated infective nymphs of a related porocephalid, *Porocephalus crotali*, are killed, freely migrating nymphs erupt through the epidermis 24 to 48 hours after death (Riley, unpublished observations). Here nymphal behaviour is directed towards liberation into the stomach and thence into the body-cavity of the rattlesnake definitive host.

An unusual feature of mature infections of *K. coarctatus* and *K. pattoni* is the absence of males. In nymphal infections the sex ratio is unity (Hett, 1924; plus unpublished observations) whereas in mature infections males are virtually absent: only five mature males (approximately 30 mm long) were recovered compared to over 200 females (of equivalent or greater body length). During development males undergo precocious sexual development and copulation occurs when females are immature—this may be obligatory because copulation has never been observed at any other time (Hett, 1924) and the penis is probably inserted directly into the spermathecae which, being positioned at the junction of the ovary and oviduct, become progressively more remote from the vagina as the uterus develops

and elongates. After insemination, males die and females store sperm for the duration of the pre-patent and patent periods. Since females can live for years this explains the odd sex ratio.

Acknowledgements

J. Riley is greatly indebted to the Royal Society and the Carnegie Trust for grants towards this research. We also thank Mr. K. H. Hyatt of the Arachnida Section and Mr. A. F. Stimson of the Reptile Section, both of the Department of Zoology, British Museum (Natural History) for their respective help in making the pentastomid collection freely available and for invaluable assistance with reptile nomenclature. Finally we wish to thank Miss M. Benstead for her painstaking care with the drawings.

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Accepted for publication 25th July, 1979.