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BIOGEOGRAPHIC IMPLICATIONS OF EVOLUTIONARY TRENDS IN ONYCHOPHORANS AND SCORPIONS

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ABSTRACT.- A comparison with another group of terrestrial predatory invertebrates, the Order Scorpiones, suggests that the lack of adaptations to city microenvironments has been the central limitation to further biogeographic radiation in the phylum Onychophora.

KEY-WORDS.- Evolution, Ecology, Biogeography, Onychophora, Scorpions

RÉSUMÉ.- Une correlation entre des Onychophores et un autre groupe d’invertCbrés terrestres predateurs, l’ordre Scorpiones, suggère que l’absence d’une adaptation aux microenvironnements andes a été le principal facteur limitant d’une plus ample radiation biogeographique du phylum Onychophora.

MOTS-CLES.- Evolution, Ecologic, Biogeographic, Onychophora, Scorpions

INTRODUCTION

A recent cladistic analysis of Cambrian, Carboniferous and extant onychophorans suggested the existence of a common ancestor with armoured plates, an annulated body and long oncopods (‘legs) as well as later taxa with radically different body characteristics, possibly as adaptation to life in reduced spaces (MONGE-NAJERA, 1995). Furthermore, physiological details are consistent with the hypothesis that these animals colonized land via the littoral zone. This may have prevented the type of xeric habitat adaptations that played a role in the large geographic and taxonomic radiation of insects, for example (MONGE-NAJERA, 1995).

The comparative method is useful to examine evolutionary trends such as those mentioned above, but the selection of a proper comparative taxon is very important for a meaningful analysis. Scorpions seem appropriate because, like onychophorans, they are an old group of invertebrate predators which has not radiated taxonomically to the extend of insects (see POLIS, 1990; LOURENÇO, 1994).

The present paper, based on a variety of biological characters, compares both groups. Scorpion and onychophoran characteristics were tabulated from several sources detailed with Appendix I.

SIMILARITIES BETWEEN ONYCHOPHORANS AND SCORPIONS

The analysis of Appendix I indicates that scorpions and onychophorans share several characteristics, such as bodies adapted to life in small spaces and thus small enough to operate with open circulatory systems. Both prevent dehydration by becoming active during the night. They have an endogenous circadian rhythm and wheneverpossible hunt near the entrance of a burrow, avoiding hard-bodied or dangerous prey. At least some preoral digestion is known in the two groups, which can survive prolonged periods without food. Both are restricted to relatively predictable microclimates, are not greatly affected by vegetation type and survive in their burrows or caves when their habitat is being burned. While reproductive diapause may be frequent in scorpions and onychophorans, parthenogenesis and theratological malformations are reported to be infrequent in both.

Other similar characteristics are longevity, gestation time and the ability of females to store semen, needing only one insemination in their lifetime, while males mate several times. Larger females of the two taxa have bigger litters while litter size is negatively correlated with the body size of young. Finally, both share high mortality rates shortly after birth (with important exceptions in scorpions) and an initial 1:1 sex ratio which skews toward females because of higher male mortality. Both seem to have populations of similar densities which do not fluctuatly greatly in mumbers.

DIFFERENCES BETWEEN ONYCHOPHORANS AND SCORPIONS

The physiology of onychophorans, less adapted to resist dehydration, is characterized by a tracheal system which cannot be closed and by the elimination of uric acid and moist fecal matter. They are absent from arid zones and occupy a narrower altitude range and burrows which are more constant climatically (Appendix I). Furthermore, they walk more slowly and a greater proportion of the population becomes active every night. When a prey is found, relatively more of it is ingested and it cannot be moved to the safety of the burrow for consumption.

Onychophorans develop more rapidly (moulting more often), reproduce while younger and have smaller litters, investing more in each young. Adult mortality rates are lower.

EVOLUTIONARY TRENDS

The biology of onychophorans is even less known than that of scorpions; thus this analysis is based on the assumption that the few onychophoran species to which this compilation applies are representative. This is reasonable because the phylum is relatively homogeneous in what is known about its morphology, physiology and basic behavior (RUHBERG, 1985; MONGE-NÁJERA *el* a!., 1993; MONGE-NÁJERA and MORERA, 1994; MONGE-NAJERA, 1995).

In comparison with scorpions, onychophorans are an older but less diverse taxon, even if the number of described species increases two- or threefold after biochemical reanalysis, as seems possible in the light of recent findings (RUHBERG, 1992). Favored hypotheses suggest that the number of species should be higher in taxa that are older, have smaller body size or bear ovipositors (ZEH *et* al., 1989). The differences in biodiversity of onychophorans and scorpions are not in accordance with these hypotheses.

Apparently onychophorans colonized land via the littoral zone, not the freshwater habitat (MONGE-NÁJERA, 1995), which may be the origin of most ecological differences, because the resulting physiology is poorly adapted to arid microhabitats (MONGE-NÁJERA, 1995). Onychophorans are more restricted geographically and are limited in their movements to the close range of appropriate burrows. Curiously this has not produced great reproductive differences, apart from the smaller litters and marked precociousness of onychophorans.

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APPENDIX 1

Comparison of ecological characteristics in the order Scorpiones and the phylum Onychophora (sources listed at end of table).

	Scorpiones	Onychophora
GENERAL DATA AND ADAPTATIONS		
Number of described valid species	1300	85
Earliest known fossils	Silurian	Cambrian
Time of land colonization	Carb-Trias.	Ordovician?
Via of land colonization	Freshwat?[1]	Littoral?
Lower and higher lethal temperatures (°C)	-12 to 45	Near 0-30
Circulatory system	Open	Open
Respiratory structures	Book lung	Tracheae
Sodium/potassium mechanism of hydric equilibrium	Present	Probably
Malpighian tubules	Present	Absent?
Coxal glands	Present	Present
Nephrocytes	Present	Present
Lymphatic glands	Present	Absent?
Basic excretoly product	Guamne	Uric acid
Fecal material	Dry	Moist
Water loss	0.025-1 $mg/cm^2/hr$	0.08-2.0 1 %/min
Relative non-lethal water loss in %of body weight	30	39
Time that can survive at 0 RH	7 days	<7mm
Water loss increases at higher temperatures	Yes	Yes?
Can decrease O_2 consumption to reduce water loss	Yes	?
Rate of water recovery from air or substrate (°/dmin)	0.0 13	0.43-3.8
Body contents (%) of water at birth 80	80	?
Water content of prey (%)	50-80	?
Metabolic rate (mmO_2/g/hr, 25C)	35-123	?

[1] There is sonic disagreement among authors about a marine versus a freshwater route of colonization (see Pous 1990, SHEAR and KUKALOVA-PECK 1990)

HABITAT ECOLOGY

Predictable environment	Yes	Yes
Altitudinal range (m)	0-5500	0-3000
Individual size at higher sites	Smaller	Smaller/or bigger
Individuals from dry areas smaller	Sometimes	?
Has colonized desert areas	Yes	No
Some species adapted to cave life	Yes	Yes
Species found today in littoral habitats	Yes	No?
Arboreal life developed in some species	Yes	Yes
Soil type correlated with distribution	Yes	Yes?
Taxonomic structure of vegetation important in spatial distribution	No	No
Taxonomic structure of vegetation important in global distribution	Yes	No
Dorso-ventral compression of body and short legs allow life in small spaces	Yes	Yes
Communal behavior in patches of favorable microclimate	Yes	Yes
Adults (especially males) travel at greater distances from burrow	Yes	Yes
Field undisturbed speed (cm/mm)	76	2.4-3.9
Can survive in periodically burnt habitat	Yes	Yes
Maximum depth of burrow (cm) 100 50	18	2.6
Thermic fluctuation in burrow, as % of external fluctuation		
Humidity fluctuation in burrow, as % of external fluctuation	16	?

SENSES

Can detect other animals by air or substrate vibrations	Yes	Yes
Able to detect small humidity differences	Yes	No?
Thermophilic	Often	Rarely?
Photonegative, active mainly in dark	Yes	Yes
Orientation by objects and starlight	Yes	?
Detail of image produced by eye	Low?	Medium?
Perception of UV light	Yes?	?
Most activity in first half of night	Yes	Yes
Endogenous circadian rythm	Yes	Yes
Seasonality based on thermal clues	Yes?	?

TROPHIC ECOLOGY

Species interactions important	Yes	Probably
Specialized, narrow niche	Yes	Yes
Proportion (%) of population active onanyonenight	5-15	Near47
Proportion (%) of population that feedsinanyonenight	1-8	Near5O
Proportion (%) of nights the individual leaves burrow	<=60	24-67
Normal hours per day outside the burrow	<4	0.27-1.6
Fidelity to burrow	High	Not high
Often hunt from entrance of burrow	Yes	Yes
Heavily sclerotized or dangerous prey normally avoided	Yes	Yes
Prey size correlated with body size	Yes	Yes
Dead prey normally refused	Yes	Yes
Are ambush predators which optimize use of chemical weapon	Yes	Yes
May cany prey to burrow for consumption	Yes	No?
Takes advantage of weak body parts to penetrate prey	Yes	Yes
Weaker individuals avoid cannibalistic members of the taxon in time or space	Yes	?
Females sometimes consume sexual partners	Yes	?
Use same chemical to hunt and for defense	Yes	Yes
Produce striduiation or substrate vibrations as warning or in courtship	Yes	No?
At least some pre-oral digestion	Yes	Yes
Digestion time (hrs)	1 to several	18
Weight increase (%) after a large meal	16-33	10-80
Food stored in hepatopancreas	Yes	No
Months that can survive without food	l-12[2]	1-8
Moulting, mating and birth often in burrow	Yes	Yes?
Ecotypic crypsis as protective coloration	Yes	No?
Suffer parasization by nematodes	Yes	No?
Are attacked by parasitoids	No	No?
Proportion (%) of population with acari	3-42<	?
Normal number of acari per host	20-30<	?

REPRODUCTION

Types of reproduction	Viviparity	Oviparity Ovoviviparity Viviparity
Parthenogenesis known in the group	Yes	Yes
Reproductive seasonality	Present	Present
Sexes brought together via pheromones	Yes	Probably
Sex of leader in courtship and mating	Male	?
Females often heavier than males	Yes	Yes
Consumption of spermatophore by females and or males	Yes	Yes
Some males insert vaginal plugs	Yes	Unnecessary in most spp.
Males mate more than once	Yes	Yes
Females mate more than once	Yes	Some
Females can reproduce more than once	Yes	Yes
One insemination may produce multiple broods	Yes	Yes
Gravid females can mate	Yes	Some
Starved females can resorb embryos	Yes	Yes ?
Gestation (months)	2-24	6-14
Age at first reproduction (months)	6-48	Males 0.25?-l 1 Fem. (x) 15-30
Synchrony in parturition.	Present	In some?
Duration of parturition (hr)	1-24	*0.25-0.75*
Theratological malformations	Not rare	Rare
Litter size (often equal to fertility measured as offspring/year)	1-105	1-53
Larger mothers have larger litters	Yes	Yes
Larger litters may have smaller young	Yes	Yes
Days the young remain with mother	3-20	1-few
Young do not feed for several days	Yes	Yes
Young with high water loss and gain water from body contact with mother	Yes?	?
Mother recognizes offspring chemically	Yes	?
Young can be cannibalized by adults	Yes	?
Duration of first instar (days)	1-14	< 13
Number of molts throughout life	4-9	93-140
Time between molts	1?-1 1 months	12-25 days
Maximum female molts before maturity	9	47
Minimum male molts before maturity	4	4
Age to maturity (months)	6-83	2-19
Males mature earlier than females	Sometimes	Often
Longevity (years)	2-25	1-7

[2] A 12 month starvation limit may be an exaggeration

POPULATION BIOLOGY

Fligh mortality shortly after birth	Yes	Yes
Low mortality of inmatures	Yes	No?
High mortality of adults	Yes	No
Sex ratio at birth near 1:1	Yes	Yes
Adult sex ratio often female-biassed	Yes	Yes
Male-biassed ratios can result from cannibalistic males	Yes	?
Population increase rate	1.5-7	?
Parental investment (as % of body weight)	11-45	8-85
Total female output (offspring/lifetime)	e.g.70[3]	6-48
Density dependent mortality common	Yes	Yes?
Small population flucttions	Yes	Yes
Density (individuals/m)	0002-12 0	05-1
Biomass (kg/Ha)	1.23-20	8.3
Prey biomass (kg/Ha)	Above 12	?

Table sources: LAVALLARD and CAMPIGLI 1975; LAVALLARD *et at.*, 1975; RUHBERG and NUTTING, 1980; READ, 1985; RUHBERG, 1985; KOVOOR *et* at., 1987; READ and HUGHES, 1987; CAMPIGLIA and LAVALLARD, 1989; POLLS, 1990; L0URENÇ0, 1992, 1994; L0URENÇ0 and CUEUAR, 1994; MONGE-NAJERA, 1994a,b, 1995; MONGE-NAJERA and MORERA, 1994; MONGE-NAJERA *el* at., 1993.

[3] Range may exceed 4-200