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Source: Journal of Orthoptera Research, 18(1) : 1-4

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/034.018.0105

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# On the significance of changes in pterothoracic sternal morphology within the Vilernae (Ommatolampinae, Acrididae)

Accepted January 15, 2009

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**Abstract**

The Nicarchi (*sensu* Descamps 1976) are a group of flightless genera within the Vilernae, characterized by living on trunks of trees and by a series of mostly adaptive morphological features. They also have relatively wide thoracic sternal interspaces. It is shown here that this last is due to two processes: development of relatively wider thoraces and reduction in the size of the sternal lobes. The latter correlates with loss of flight and of the wings, as shown by a series of genera from within the Vilernae, and is associated with the atrophy and/or loss of the indirect flight musculature. A probable selective advantage of both processes is to increase the space available for the crop, the major organ of food storage and digestion.

**Key words**

Vilernae, flight, sternum, brachyptery, gut

Brunner von Wattenwyl (1893: 139) originally used the name Nicarchi for a group of three genera *(Nicarchus, Antiphanes, Demonax*) within his subtribe Vilernae Brunner von Wattenwyl, 1893. This usage was followed by Giglio-Tos 1897, p. 48, who included three further genera (*Cocama, Anablysis and Hypsipages*). Descamps (1976) reused and redefined this name, in the light of modern systematics. In it he placed eight genera (*Nicarchus, Hypsipages, Aptoceras, Rhabdophilacris, Sclerophilacris, Bryophilacris, Acridocryptus, Sciaphilacris*), and later (Descamps & Rowell 1984) added a ninth (the then newly described *Cryptacris*). This group is characterised by the following features:

1. cryptic coloration, mimicking mosses, lichens or bark
2. an exaggerated rugosity of the cuticle, sometimes including the development of bizarre spines and processes over the entire body (*e.g.*, *Nicarchus*, *Hypsipages*)
3. eyes strongly protuberant
4. disc of the pronotum with bumpy projections between the 2nd and 3rd sulci
5. meso- and metasternal spaces very wide, especially the metasternal lobes widely separated
6. antennae often nodular
7. 6 or 7 external spines on the hind tibia (always 7 in other members of this tribe)
8. all but one (*Sciaphilacris*, which is the least modified of all the assemblage in other respects as well) are flightless.

Many of the above characters are apparently related to the life style of the group. The insects are "dendrosclerophiles", in Descamp's terminology, living on the trunks and major branches of living or dead trees; they live in the tropical forests of the Amazon basin or Central America. (Most of the remaining Vilernae are "phryganophiles", living in sunny situations in forest light-gaps or forest edges.) Arguably characters 1, 2, 4 and 6, above all else, serve to increase concealment from visual predators. Flightlessness and protuberant eyes are both very common in tropical forest grasshoppers, and the reasons for this have been discussed elsewhere (*e.g.*, Rowell 1978). The slightly lower number of spines on the hind leg is a relatively trivial character, which does not demand an adaptive explanation. One is left with character 5, the wide meso- and metasternal spaces. Is this simply a phyletic trait, assuming that the Nicarchi are in fact a monophyletic group within the Vilernae? [Descamps (his fig. 1) explicitly thought they were; but there is no compelling evidence, and they might equally well be an assemblage of ecologically convergent forms; there are, *e.g.*, marked differences within the group in the structure of their spermathecae (pers. obs)]. Or could there be another explanation for this pervasive aspect of their morphology?

While recently reviewing the Central American Vilernae I prepared drawings to compare the pterosternal morphology within the group. The genera used are listed with pertinent information in Table 1. Fig. 1 shows the situation in six genera: the Central American *Nicarchus, Cryptacris, Vilerna,* and *Leptomerinthoprora,* and the Amazonian *Locheuma* and *Sciaphilacris*. Descamps and Amedegnato (1989a,b) considered *Vilerna* and *Locheuma* to be very closely related, and noted that also *Leptomerinthoprora* and *Sciaphilacris* share many characters with them. It is immediately clear from the Figure that two (*Nicharchus* and *Cryptacris*) of the three Nicarchi shown have indeed much wider thoracic interspaces than the rest, as Descamps observed; *Sciaphilacris* does not. The same drawings have been scaled to constant length in Fig. 2, and this makes it obvious that the thoraces vary considerably in their relative width. The actively flying *Vilerna* has a long slim thorax, whereas *Nicarchus* and *Cryptacris* have short wide ones, with the others intermediate. This raises two questions: why do the Nicarchi have wider thoraces, and to what extent is the extra size of the nicarchan thoracic interspaces merely a reflection of this increased width?

To address the second question, Fig. 3 shows again the same drawings, now "morphed" with the computer to constant length **and** constant width. Strikingly, the thoraces now fall into three groups: the actively flying *Vilerna* with narrow interspaces, the apterous *Cryptacris* with wide ones, and the brachypterous (*Nicarchus, Leptomerinthoprora, Locheuma*) or alate-but-inactive (*Sciaphilacris*) remainder, with essentially identical intermediate morphologies. After scaling, *Nicarchus* is no longer very different from other brachypterous forms (*Leptomerinthoprora, Locheuma*).



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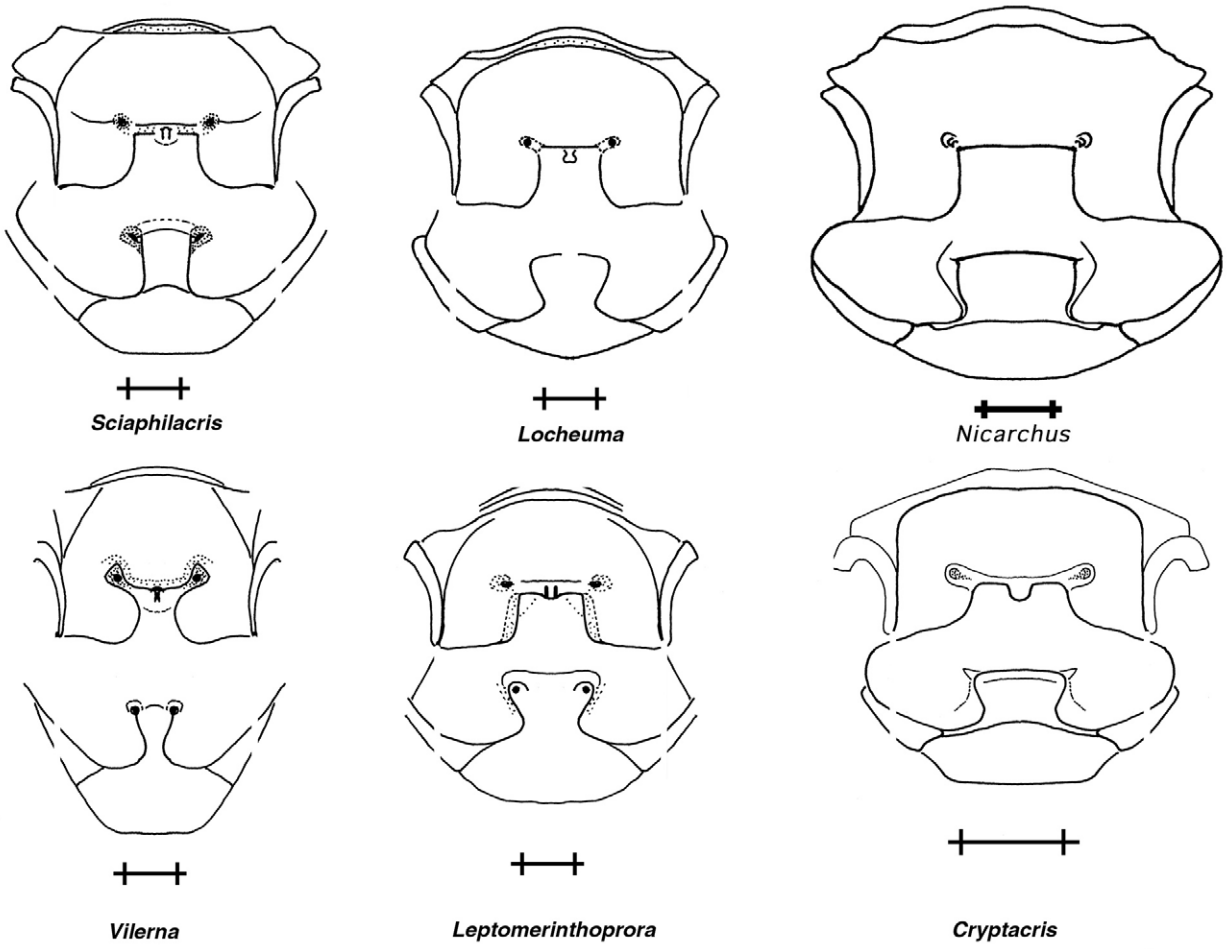



**Fig. 1.** Drawings of the pterosternal morphology of the six taxa listed in Table 1. Scale bars 1mm throughout.

There is thus a good correlation of the development of the sternal lobes and interspaces with flight. A narrow interspace implies relatively larger lobes, and a wide one, smaller lobes. This makes sense if one considers the internal musculature of the pterothorax. The powerful dorsoventral indirect flight muscles attach to the sternum mediolaterally, while the direct flight muscles attach laterally. Many of the latter are bifunctional muscles, which also insert on the coxal bases and function in walking and climbing (Snodgrass 1929, Wilson 1962). Consequently a powerful flier needs wide lobes and thus a narrow interspace, whereas an insect which has long lost its wings, such as the apterous *Cryptacris*, can reduce or lose completely the indirect flight musculature, but needs to retain most of the direct musculature. The brachypterous insects, which have presumably had less evolutionary time in the flightless condition, are intermediate; *Sciaphilacris*, though still alate, is "behaviorally brachypterous", flying rarely, and has apparently made the same muscular adjustment as the morphologically brachypterous species. Fig. 3 also shows that *Cryptacris*, and only that apterous genus, has also moved the internal sternal apophyses laterally outwards, away from the midline.

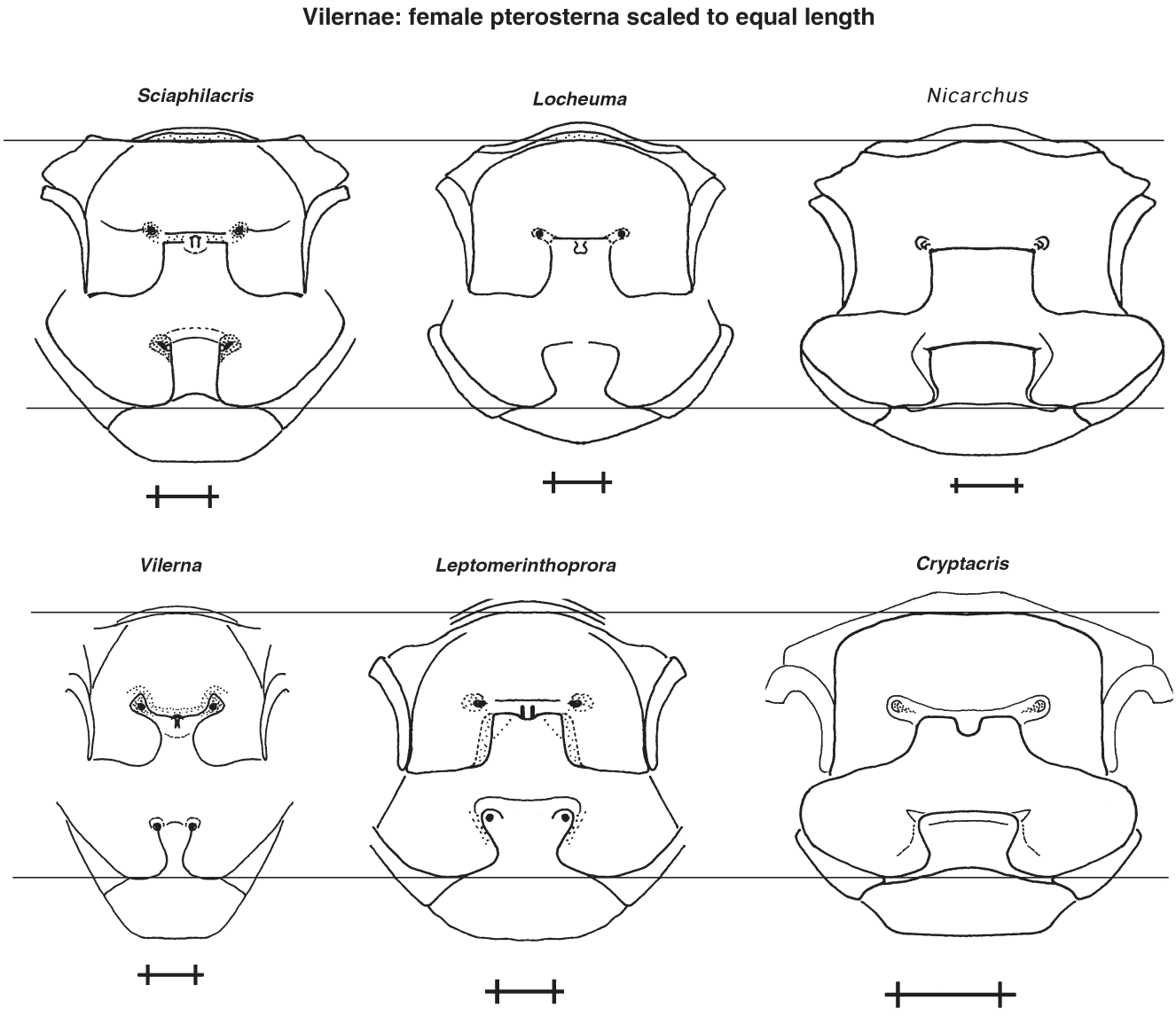
What do flightless grasshoppers do with the increased space in the center of their pterothorax? They use it for a larger gut. The crop, the major organ of food storage and digestion, is much wider in such insects, and can reach dramatic proportions in, *e.g.*, the polyphagous apterous bactrophorine genus *Rhicnoderma*. I have not yet examined the gut of *Cryptacris* because of the paucity of specimens available, but I predict that its crop will be found to be proportionately wider than that of *Vilerna*. This may also be a further factor in explaining why the flightless Nicarchi tend to develop wide thoraces overall, apart from their reduction of the sternal lobes. *Nicarchus* itself feeds on moss (pers. obs., faecal analysis), a rather unpromising diet (Forman 1968), and especially under these circumstances, extra

**Table 1.** The taxa discussed in this article. All are members of the subtribe Vilernae of the Ommatolampinae; the first three are grouped within the Nicarchi *sensu* Descamps.

| Genus | Species figured | Nicarchi *sensu* Descamps? | Wing condition | Metasternal interspace | Provenance |
|---|---|---|---|---|---|
| *Cryptacris* | *costaricensis* | yes | apterous | very wide | C. America |
| *Nicarchus* | *erinaceus* | yes | brachypterous | very wide | C. America |
| *Sciaphilacris* | *alata* | yes | alate but inactive | fairly narrow | S. America |
| *Locheuma* | *brunneri* | no | brachypterous | intermediate | S. America |
| *Vilerna* | *polita* | no | alate, active | narrow | C. & S. America |
| *Leptomerinthoprora* | *brevipennis* | no | brachypterous | intermediate | C. America |



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| | | |
|---|---|---|
| **Alate - inactive** Nicarchi | **Brachypterous - active** | **Brachypterous - inactive** Nicarchi |
| **Alate - active** | **Brachypterous - active** | **Apterous - active** Nicarchi |

**Fig. 2.** Drawings of Fig. 1 scaled to a constant length. Scale bars 1mm throughout.

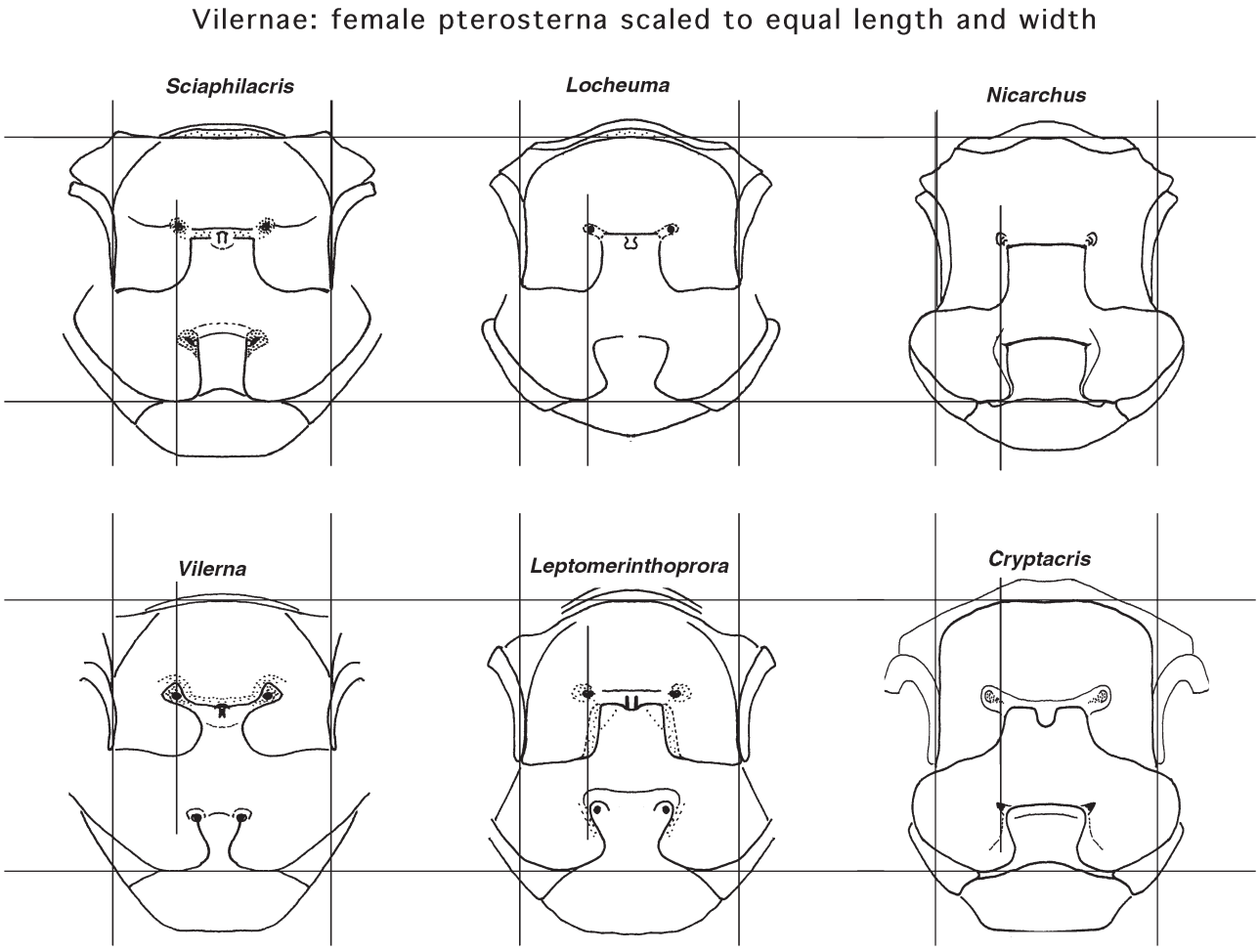
storage and digestive capacity can be no bad thing. It may even be that the advantages of a larger gut could represent yet another selection pressure to favor the preponderance of flightless grasshoppers (Rowell 1998) in the chemically diverse rainforest environment, in addition to those previously suggested.

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| | | |
|---|---|---|
| **Alate - inactive** Nicarchi | **Brachypterous - active** | **Brachypterous - inactive** Nicarchi |
| **Alate - active** | **Brachypterous - active** | **Apterous - active** Nicarchi |

**Fig. 3.** Drawings of Fig. 1 scaled to a constant length and width.

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