clonidine was demonstrated in relatively small brainstem fragments suggests that the two sites are anatomically close to each other and may even be in the same cell. Whether such an "opioidergic" pathway is limited to the SHR or has implications for the development of hypertension in general is still unclear. Findings of a close correlation between the level of blood pressure and pain threshold in various forms of hypertension (*19*) suggest a link between some endogenous opiates and the hypertensive process.

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Thermoregulatory Significance of Thoracic Lobes in the Evolution of Insect Wings

Abstract. *The evolution of broadly attached thoracic lobes could have increased the body temperature excess of ancient wingless insects by 55 percent over that of lobeless forms. The subsequent expansion of these thoracic lobes for behavioral thermoregulation could have provided the morphological stage required for the evolution of functional wings.*

Many entomologists have speculated on the structural origin of insect wings, the possible selective pressures which produced them, and their sequential modification in the development of flight. Although most entomologists adhere to the "paranotal lobe" theory (*1*), which postulates that insect "pro-wings" were derived from nonarticulated lateral extensions of the thoracic terga (*2, 3*), reinterpretation of the juvenile wings of Paleozoic nymphs (*3*) suggests that their nymphal pro-wings were articulated structures which secondarily lost their movability by fusion with the tergum, and thus became evolutionarily convergent with "paranota" (Fig. 1).

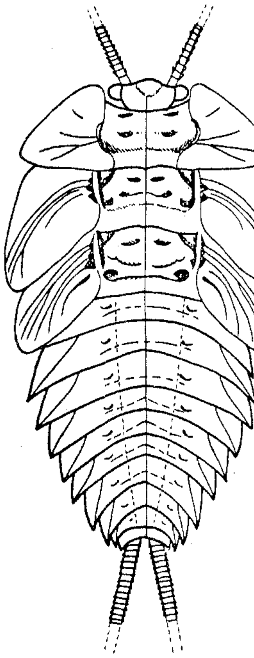

Fig. 1. Young nymph of the Paleozoic terrestrial palaeodictyopteran, *Rochdalia parkeri*, illustrating "articulated" thoracic lobes (*4*). Original reconstruction [After R. J. Wooten (*24*); from *Journal of Morphology*; reproduced with permission from the Wistar Institute].

A second major controversy has centered around the possible functions of these small, lobelike pro-wings, whether articulated or not, which likely served as the intermediate stage in the evolution of truly functional wings. These broadly attached pro-wings (hereafter termed "thoracic lobes") may have functioned originally to cover the spiracular openings or gills in amphibious ancestors (*3*), to protect and conceal insects from predators (*4*), to facilitate passive aerial dispersal by small insects (*5*), or to aid in sexual displays (*6*).

However, my experiments suggest that a more probable reason for the continued expansion of these small thoracic lobes to a critical size required for efficient gliding or flapping flight may have been their prior adaptation for behavioral thermoregulation. Because the activity of most insects is highly dependent on body temperature and the thermal conditions of their microhabitat (*7-11*), any thoracic structure that permitted the leg muscles of ancestral pterygotes (*12*) to heat rapidly and attain a higher equilibrium temperature would enhance locomotor efficiency, a condition crucial to insect survival and reproductive success (*13*).

Colias eurytheme butterflies were chosen to test this thermoregulatory hypothesis because their wings could be physically altered to approximate those of the ancestral pterygotes (*14*) and because their body length is near that of winged Protorthoptera (Paraplecoptera) with Thysanura-like immatures (*15*). In addition, preliminary temperature mapping of butterfly wings and analyses of energy exchange between wings and thorax in these butterflies showed that only the basal third of the wings were of thermoregulatory significance (*13, 16, 17*). The basal areas of *Colias* wings are approximately equivalent in size to the thoracic lobes of Paleozoic insects thought to be ancestral to modern winged forms (*3*).

Freshly killed butterflies were cooled to 10°C and suspended by a 0.30-mm hypodermic thermocouple inserted ventrally into the mesothoracic muscles. The butterflies were positioned with wings perpendicular to incident radiation from a 150-W Duro-Lite lamp and received approximately 60 mW cm^{-2}, an irradiance well within the normal range received by a horizontal surface during a typical summer day in the temperate zone.

Fine pins impaling *Colias* wing fragments equivalent in size to ancestral thoracic lobes, were held by two aluminum clips mounted on a balsa platform. The clips holding the pins with wing fragments could be rotated away from the suspended body without disturbing the position of the insect body or the experimental conditions. Air stagnation in the room was prevented during the heating and cooling experiments by circulating air at approximately 10 cm sec^{-1}, a wind velocity that produces minimal forced convective heat loss (*9*). Relative humidity remained near 50 percent and ambient air temperature was 22.5° ± 0.5°C. Thoracic temperature (to ± 0.1°C) measured by the hypodermic probe was registered on the biological scale of a Bailey Bat-8 amplifying thermometer and monitored by a Bausch & Lomb VOM-5 chart recorder (*18*).

A representative experimental series shown in Fig. 2 illustrates the thermoregulatory effect of black thoracic lobes constructed from the basal portions of *Colias* wings 5 mm in length by 3 mm in width. When the lobes are pressed to the thorax of a *Colias eurytheme* body 15 mm in length, a difference between body temperature and ambient temperature (ΔT) of 20.8°C is attained in a horizontal position, whereas a ΔT of 17.8°C is achieved in a vertically oriented position. However, the same body reaches a ΔT of only 13.4°C without the thoracic lobes. Subsequent heating experiments on the same individual under identical experimental conditions show that ΔT values were reproducible to within ± 3 percent of the original values (*19*). Thus, butterflies with 5 by 3 mm thoracic lobes attain a ΔT nearly 55 percent higher than butterflies without lobes.

The available fossil evidence indicates that all Paleozoic pterygotes had very broadly attached, dark, or obliquely striped wings with the darkest portion lying adjacent to the thorax (*3*). The experimental data with broadly attached thoracic lobes shows that thoracic prowings would have conferred a similar thermoregulatory advantage on a diurnally active, terrestrial, ancestral pterygote. Low metabolic rates of heat production in contemporary apterygotes (*20*) suggest that the physiological and locomotor activities of the ancestral forms also were determined largely by ambient thermal conditions. Thus, a behavioral thermoregulatory strategy such as basking was likely the only reliable method of elevating thoracic temperature during cool thermal periods. Basking is an energetically inexpensive means of thermoregulation that permits efficient and rapid locomotion in many contemporary insects without the physiological burden required by endothermy (*13, 17*). Because the muscles concerned with locomotion in the ancestral insects were located in the thorax, it is this region that would have benefited directly from the enlargement of any structure that could be used for thermoregulation. However, the abdominal plates present on many forms of Paleozoic nymphs and adults could have further increased the thermoregulatory capabilities of these ancestral pterygotes.

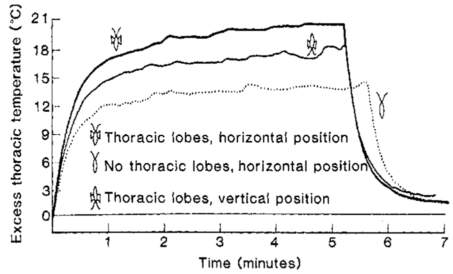

Fig. 2. Comparison of excess thoracic temperature (ΔT) using a *Colias eurytheme* body 15 mm in length. In a horizontal basking position, the body supplied with thoracic lobes (5 by 3 mm) constructed from *Colias* wings achieves a ΔT 55 percent greater than the same body without lobes.

The ability to thermoregulate efficiently under conditions of low ambient temperature or low radiant energy (*21*) would have had many advantages (*22*). Any broadly attached thoracic structure would have increased an insect's characteristic dimension or effective diameter, its thoracic mass and heat capacity, and the thoracic surface area capable of absorbing radiant energy. By remaining close to the basking substrate, ancient insects could have trapped pockets of warming air beneath their thoracic lobes while simultaneously disrupting the airflow across the thorax and thereby reducing convective heat loss (*23*). The resulting increase in ΔT would have been incurred at no additional metabolic cost to the insect. Greater activity would have permitted longer foraging periods under thermally cool conditions, quicker escape from predators, and increased competitive ability for mates. Greater individual activity also would have translated into greater dispersal opportunities for the species. Given certain environmental conditions and basking behaviors, the conclusion is that these broadly attached thoracic lobes would have aided in heating the thoracic muscles of ancestral pterygotes.

The selective advantage for thermoregulation does not exclude other possible functions previously mentioned which may have evolved concurrently with the selective process of expanding small thoracic lobes for thermoregulation. As thoracic lobes became progressively larger for thermoregulatory purposes, a physical size limit was reached whereby no greater heating advantage could be obtained by any further increase in lobe length. This size limit is approximately 10 mm in wing length for a butterfly 15 mm in body length (*16, 17*). Wings of greater size confer little additional thermoregulatory advantage. However, thoracic lobes of this length in ancestral pterygotes could have been used in conjunction with the long anal cerci and caudal filament to perform gliding maneuvers from the tall vegetation of the Devonian, and would have set the morphological stage necessary for the evolution of truly functional wings.

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ed when no further thoracic temperature increase was recorded for 2 minutes.

19. In other experiments, intact butterflies with basally blackened wings or black wing stubs equivalent to the basal third of the wings (approximately 10 mm) attain a ΔT nearly 75 percent higher than wingless butterflies. In addition, paper wings cut from black construction paper and size-matched to *Colias* wings performed as well as real wings. Although some energy is transferred from the wing bases to the thorax via conduction and radiation, most of the wing-mediated increase in body temperature is due to the wings' capacity for reducing convective heat loss by trapping warmed air beneath the wings and by increasing the effective diameter of the thorax (*16*, *17*).
20. Contemporary apterygotes thought to be cladistically closest to the ancestral pterygotes are the lepidotrichid thysanurans (*14*), the members of which are thermal conformers, incapable of elevating thoracic temperature by endothermy. Efficient muscular thermogenesis in insects occurs only in those with larger thoracic mass (*17*) or those with high ratios of body weight to wing area.
21. Cool environments might be due to a combination of low ambient temperature, low levels of solar radiation, and high winds such as during times of low solar angle or intermittent cloudy weather. Cool environments also include those resulting from seasonal changes or altitudinal and latitudinal effects.
22. The thermoregulatory hypothesis is also supported when the environment of the ancestral pterygotes is reconstructed. Forms ancestral to insects evolving during the Upper Silurian likely inhabited rainy swamps with discontinuous patches of terrestrial vegetation dominated by the Psilophyta [B. M. Mamajev, in *Proceedings of the 13th International Congress of Entomology* (Moscow, 1968) (Nauka, Leningrad, 1971), vol. 1, p. 269] Kukalová-Peck (*3*) suggests that these ancestral insects inhabited moist niches and were semiaquatic. By the Middle and Upper Devonian, the amphibiotic ancestral pterygota had cursorial legs and long anal cerci and a medial caudal filament. When these amphibiotic insects began climbing vegetation to feed, mate, and disperse, their pro-wings were directed latero-horizontally [the most efficient position for thermoregulation by baskers (*7*, *17*)], and these forms—like modern Apterygota (for example, Thysanura)—had an incomplete development without a metamorphic instar (*3*).
23. Wind velocity can be greatly reduced within the relatively stagnant boundary layer of air that envelops large objects. A dorsally ventrally flattened ancestral pterygote with lateral thoracic extensions would have experienced minimal form drag within the boundary layer in addition to being protected from forced convective heat loss [G. S. Campbell, *An Introduction to Environmental Biophysics* (Springer-Verlag, New York, 1977), pp. 2 and 73].
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Ape Language

Scarcely a decade has elapsed since we were told by the Gardners (*1*) and Premack (*2*) about the ape's remarkable capacity to learn and use a human language. Now Terrace and his co-workers (*3*), as well as others (*4*), tell us to be skeptical of those claims. This is surprising, for the main questions about how far the naturally languageless ape can learn a human language and use it in a human way have not changed in the last decade, and they still remain to be answered. Fundamentally, these questions concern what the ape can do and would choose to do with a human language in comparison to what the human child can and does.

Appropriate ape-child comparisons cannot be made by studying the ape alone; parallel studies of the human child are also needed. It is not sufficient to compare the observed characteristics of ape language with certain presumed characteristics (*5*) of child language. We need firm answers to several questions. If the ape's "talk" is cued by the human interlocutor (prompting) and is overinterpreted by enthusiastic observers (the experimenter bias), resulting in a massive "Clever Hans effect," then what is the role of these factors in the assessment of the child's language competence?

If effective verbal communication depends not only on words but also on context and situational expectations, then are not all effective human interchanges riddled with the "Clever Hans effect"? If the ape mannerlessly interrupts her interlocutor, what does a child do under similar circumstances? What does a child who says "Mommy gone to work," actually "intend" by this utterance? Would a human child brought up in a languageless environment easily learn to talk when exposed to the normal human environment? (The Indian wolf-children did not.) Does a deaf girl, trained in sign language, "talk" to her dolls while playing? What is the language competence of an autistic child who shuns human contacts but is forcibly taught a language for a couple of hours each day? Without answers to these questions, any conclusions about the significance of ape language would appear to be premature.

Clearly, an ape's level of verbal communication will not match that of a child, but might the difference between an adult's language and that of the child be of the same order as the difference between the child's and the ape's? To answer this question, we need to know a lot more about the language competence of the ape and of the child under comparable conditions. The question is answerable but not yet answered.

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4 April 1980;

The semantic and syntactic analyses carried out by Terrace *et al.* (*1*) providing evidence of structurally constrained regularities in the signed utterances of a chimpanzee are important because they support and extend earlier work (*2*-*4*). However, their evidence of nonhuman discourse patterns in apes is inconclusive and reveals how critical well-controlled environments may be to the acquisition and expression of language in these animals. Moreover, their use of information on the gorilla Koko for comparative purposes is selective and, in some instances, inaccurate and misleading.

Terrace *et al.* present data showing that Nim's mean length of utterance (MLU) failed to increase over a 19-month period (from 26 to 45 months of age), but do not mention my data (*2*) indicating an increase of 33 percent in the gorilla Koko's MLU over a similar 12-month period (from 29 to 41 months). Figures included from my publication are reported incorrectly: Terrace *et al.* (*1*, p. 891) report "the acquisition of more than 400 signs by . . . Koko." The figure I gave was 100 (*2*). They also cite (*1*, p. 895) the same article as reporting that 95 percent of Koko's two-sign combinations were interpretable into categories similar to those used to describe two-word utterances of children. The actual figure was 75 percent (*2*).

Terrace *et al.* describe (*1*, p. 899) the television program in the NOVA series entitled "the First Signs of Washoe" as "the best [example] of . . . Koko's signing." That program showed 50 seconds of film of Koko taken in 1974 by NOVA's camera crew during which she emitted three signed utterances. They state that "all of Koko's signs [in the film] were signed by the teacher immediately before . . . Koko signed." This is not true. Furthermore, no request was made to see our videotaped samples of Koko's signing.

Not included in Terrace *et al.*'s dis-