

FEEDING PREFERENCE OF *HELICONIUS ERATO* (LER.: NYMPHALIDAE) IN RELATION TO LEAF AGE AND CONSEQUENCES FOR LARVAL PERFORMANCE

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ABSTRACT. In South Brazil, female *Heliconius erato phyllis* (Fabricius) lay isolated eggs on branch tips of *Passiflora suberosa* Linnaeus, leading to early larvae first contacting young host plant tissues. These feed on young tissues, but the adaptive meaning, if any, for such an association is still unknown. In this paper, we determine what leaf ages are usually consumed by each instar, the existence of feeding preference in relation to leaf age, and the performance of *H. erato* when fed either on young or old leaves of *P. suberosa* under laboratory conditions. Freshly-hatched larvae were transferred to the terminal portion of isolated, intact shoots, and observed daily for order of leaf choice until pupation. Feeding preference in relation to leaf age was evaluated for all instars through choice tests using leaf disks from young and mature leaves. Additionally to evaluate induction of feeding preference, larvae were reared through fourth instar on either young or mature leaves and then tested using the same choice procedure. Growth performance was assessed by progressively transferring larvae, according to instar number, from intact shoots to sections where apical portion was cut off. Larvae fed starting at the terminal bud (young tissues) and moving progressively to lower leaves of increasing age (mature leaves). Larvae of all instars consumed more young leaf disks, and preference for old leaves could not be induced. Larvae reared initially on young tissues had greater survivorship and grew faster than those on mature, and this may explain the oviposition site selection and larval feeding preference of this butterfly.

Additional key words: host-plant selection, heliconian butterflies, passion vines, leaf age effects.

Heliconius erato phyllis (Fabricius) (Nymphalidae) is common in the forests of southern Brazil (Brown & Mielke 1972). It uses a number of passion vine species as larval hosts, a few being preferred in a given locality (Benson et al. 1976, Brown 1979, 1981, Ramos & Freitas 1999). Isolated eggs are laid primarily on terminal buds of *Passiflora* shoots, young tendrils and young leaves (Benson 1978, Perico 1995, Mugrabi-Oliveira & Moreira 1996a). Larvae feed initially on young leaves near the apical portion of shoots (Alexander 1961, Benson 1978). Ovipositing females reject shoots deprived of or with a damaged apical portion, and prefer to lay on large shoots compared to small (Mugrabi-Oliveira & Moreira 1996a). They also assess egg- and larval-load, and reduce daily oviposition rates under low host-plant availability (Mugrabi-Oliveira & Moreira 1996b).

There are at least three hypotheses to explain *Heliconius* oviposition and early larval feeding on young *Passiflora* tissue, which are not necessarily mutually exclusive. First, Benson et al. (1976) suggested that *Heliconius* oviposition on passion vine tendrils would help to prevent egg-predation, because eggs on tendrils are less likely to be attacked by ants. In addition, Benson (1978) hypothesized that the feeding pattern of heliconian larvae that use young tender growth, such as *H. erato*, was in part shaped by interspecific competition with species specialized on older leaves. Also, it is known that host-plant selection by phytophagous insects is linked to plant suitability as larval food (Jones 1991, Bernays & Chapman 1994). Thus, it is expected that *H. erato phyllis* oviposition on the api-

cal portion of host-plants is also related to higher suitability of the corresponding tissues as larval food.

In this paper, we address the latter hypothesis from a behavioral ecology perspective. Feeding of *H. erato phyllis* larvae and its consequences are evaluated regarding variation in leaf age on shoots of *Passiflora* (*Plectostemma*) *suberosa*. This widely spread passion vine is a primary host of *H. erato phyllis*, and one of the most abundant passion vine species in southern Brazil (Menna-Barreto & Araújo 1985, Perico & Araujo 1991, Perico 1995). Information on the phenology of *P. suberosa* and corresponding effects on *H. erato phyllis* oviposition site selection are provided by Mugrabi-Oliveira & Moreira (1996a). Specific goals of the current study are 1) to characterize the natural feeding pattern of *H. erato phyllis* larval instars in relation to *P. suberosa* leaf age, 2) to evaluate the feeding preference of each instar regarding leaf age, and 3) to determine the consequences of feeding on leaves of variable age on survivorship, growth rate and adult size.

MATERIALS AND METHODS

Insects and plants. Larvae used in the experiments came from eggs obtained from an *H. erato phyllis* outdoor insectary maintained at the Zoology Department of Federal University of Rio Grande do Sul, Porto Alegre, RS (see Mugrabi-Oliveira & Moreira 1996a). *P. suberosa* plants were obtained from cuttings that were transplanted into plastic pots. The plants originated from a population at Aguas Belas Experimental Station, Viamão County. The plastic pots were provided with 50 cm high wooden frame support for shoot growth, covered with a fine mesh cloth and maintained in an outdoor screened cage. Prior to the

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tests, plants were standardized for size by removing all branches except the main shoot in each pot. Experiments were conducted in a large laboratory chamber, adopting the prevailing abiotic conditions for the region during the summer (photoperiod 14L:10D, temperature $25 \pm 1^\circ\text{C}$, humidity $75 \pm 5\%$).

Feeding pattern. To determine larval feeding pattern in relation to leaf age, twenty freshly hatched *H. erato phyllis* larvae were individually placed on the terminal bud of healthy growing shoots bearing 12 open leaves. Additional studies that have been carried out in our laboratory (S. S. Borges & G. R. P. Moreira unpubl. data) showed that in all cases when young larvae are put on any mature leaf, they move to the tip of *P. suberosa* shoots, always starting feeding on the terminal bud. Larvae were inspected for molting daily until pupation. At each inspection, we noted the age of leaf being consumed. To make sure that molts were not overlooked, larvae were gently marked with small colored dots of enamel paint (Testors) on the dorsal part of the penultimate abdominal segment. Leaf age was determined by leaf position in relation to the terminal bud (made up of apical meristem, leaf primordia and unopen leaves) (Fig. 1A).

Choice experiments. Feeding preference in relation to leaf age was evaluated through leaf disk choice tests. Trials were conducted in plastic pots, following the methodology described in Hanson (1983). The same twenty larvae were used over all instars; corresponding rearing procedure followed that described above. Unless noted, two leaf age categories were adopted: young (consisting of the first and second open leaves on actively growing branch) and mature (sixth and seventh open leaves). Disks were cut with a cork borer (diameter of 6.75 mm; 35.78 mm^2 in area), and a fixed number offered (3, 3, 6, 12 or 18 disks of each age per larvae tested from first to fifth instar, respectively). Young leaf disks alternated with mature ones in the pot. To keep leaf disks from drying out, pots were covered with a plastic film. Leaves were collected from different plants every time. Total leaf area offered a given instar was adjusted to double the average leaf area consumed by a given instar in 5 hours (C. A. Barcellos & G. R. P. Moreira unpubl. data). All trials lasted for 5 hours, after which larvae were returned to their original rearing plants.

To evaluate possible induction of feeding preference in relation to leaf age, additional 40 larvae were reared up to third instar on young leaves. After molting to fourth instar, half of them were transferred to cuttings containing only mature leaves; the remaining 20 larvae were kept on cuttings bearing young leaves. They were all then individually tested in the fifth instar

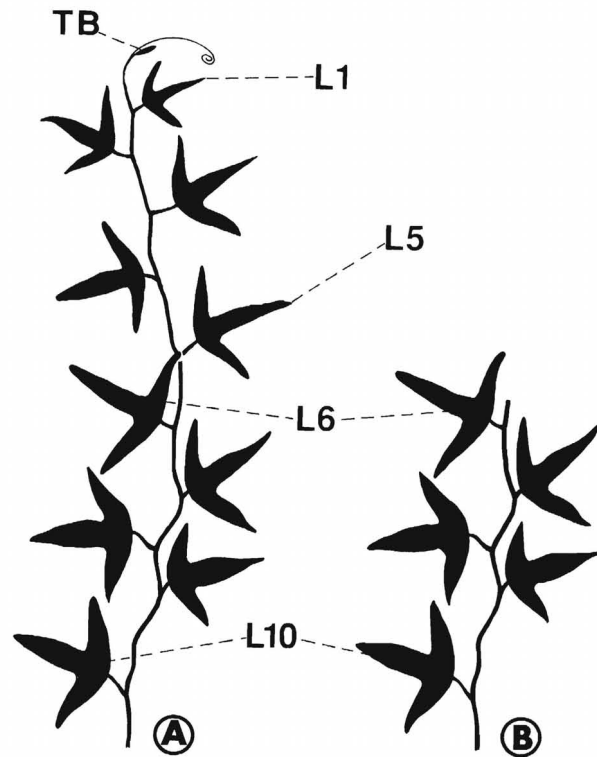


FIG. 1. Schematic representation of *Passiflora suberosa* shoots used to determine influence of leaf age on *Heliconius erato* larval performance. **A**, intact, with terminal bud and ten open leaves; **B**, lower section, with five mature leaves (terminal bud and five apical open leaves were cut out). **TB**, terminal bud; **L**, open leaf. Numbers indicate position in relation to shoot apex. Tendrils and stipules associated with open leaves were not drawn.

using the leaf-disk choice test described above (18 disks of each age per larvae).

Feeding was measured as area of disk eaten, recorded by placing the disks against graph paper at the end of each feeding trial and counting the number of square millimeters corresponding to the missing leaf area. If only young leaves were damaged, or over twice the area of young as mature leaves was consumed, larvae were scored as having discriminated in favour of young leaves. Conversely, if only mature leaves were consumed, or over twice the area of mature as young leaves was missing, then larvae were scored as having chosen mature leaves. Feeding trials were recorded as neutral when neither leaf-age category had more than twice the damage of the other (see Thomas 1987). To test the hypothesis that consumption of young leaves was greater than mature, scores were tested using one-tailed sign tests, following the procedure described in Conover (1980).

Larval performance and adult size. To determine leaf age effects on performance, larvae were in-

TABLE 1. Experimental scheme adopted to test influence of *Passiflora suberosa* leaf age on *Heliconius erato* larval performance. Treatments correspond to numbers of instar staying on intact shoots.

Treatment	Shoot type offered as food	
	Intact	Lower section
0		all instars
1	instar I	instars II-V
2	instars I and II	instars III-V
3	instars I-III	instars IV and V
4	instars I-IV	instar V
5	all instars	

dividually reared on potted plants receiving one of the following shoot types: 1) intact, with ten leaves and terminal bud; 2) lower section, with five mature leaves (terminal bud and five apical open leaves were cut out)

(Fig. 1). Six different treatments were used. Larvae were transferred from plants with intact shoots (type 1) to those with mature leaves (shoot type 2) according to instar completion (Table 1). For example: "In treatment 0, larvae were placed directly on shoots with mature leaves; in treatment 5, larvae were allowed to complete all five instars on intact shoots". A completely randomized block design was adopted; the experiment was carried out ten times (dates = block effect), one replicate per treatment was conducted on each occasion. Since there was no block effect, data were treated within an one-way design (10 replicates per treatment). Larvae were checked daily for molting until death, or up to emergence to the adult stage. Forewing length of freshly emerged adults was measured with callipers. Data from development rates

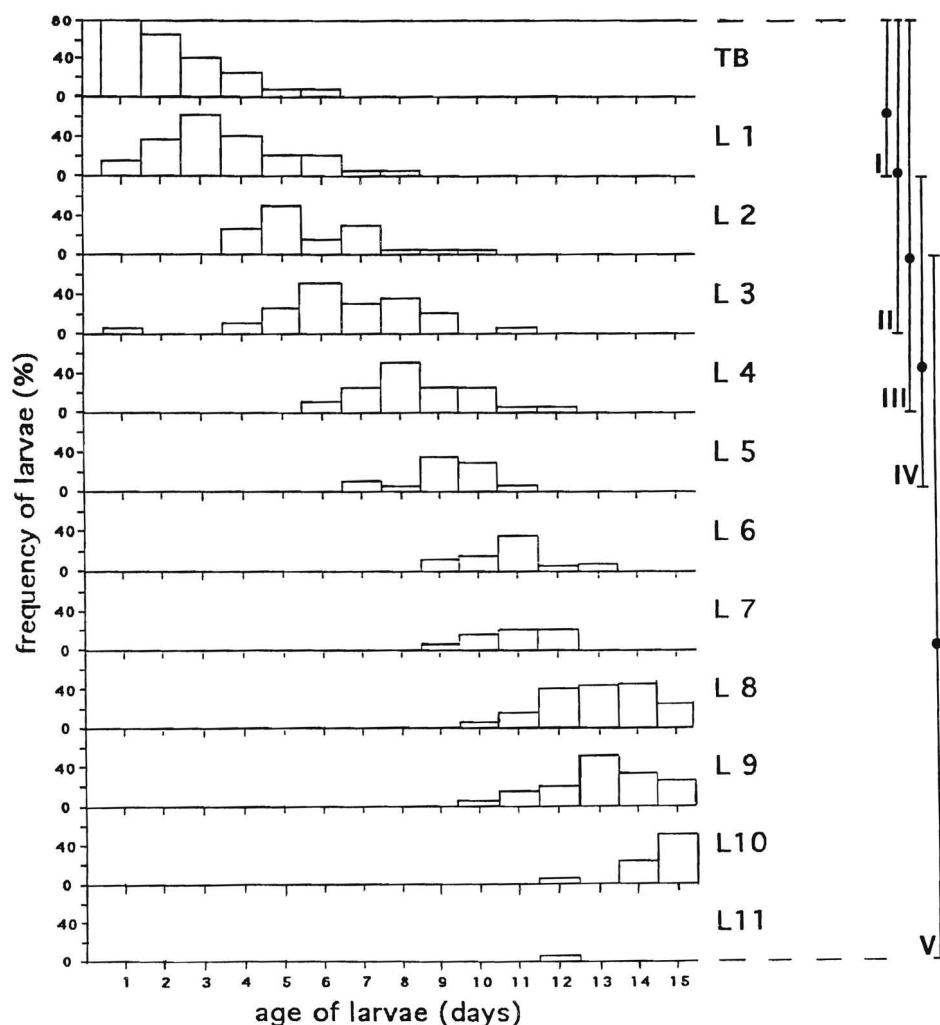


FIG. 2. Sequential feeding pattern of *Heliconius erato* larvae ($n = 20$) in relation to *Passiflora suberosa* leaf age and instar number. **TB**, terminal bud; **L**, open leaf. Arabic numbers designate position of leaf in relation to shoot apex. Roman numbers represent larval instars. Closed circles and associated bars denote the median and corresponding interval of leaf age eaten by a given instar.

TABLE 2. Selection by different instars of *Heliconius erato* larvae ($n = 20$) for young vs. old leaves of *Passiflora suberosa*. Data show number of larvae falling into each preference category. See text for description of discrimination categories.

Instar	Preferred leaf category			p*
	Younger	Neutral	Older	
I	20	—	—	< 0.001
II	19	1	—	< 0.001
III	18	1	1	< 0.001
IV	18	1	1	< 0.001
V	9	9	2	< 0.04

* probabilities calculated from sign tests.

were log transformed for the analysis of variance, following the criteria described in Sokal and Rohlf (1981). Differences among treatments were tested using Fisher's Protected Least Significant Difference multiple comparison tests, when analyses of variance were significant.

To determine specific effects of leaf age on adult size, 40 additional larvae were tested. These were reared on young leaves up to third instar, and after molting for the fourth instar, half of them were kept feeding on young leaves while the remaining fed on mature leaves until pupation. After emergence, adult forewing length was measured, and data were compared through unpaired, two-tailed *t*-tests. There was no indication that size of males and females differed in these experiments, and thus data were grouped. Unless noted measurements are given as mean \pm standard error.

RESULTS

In general, the larvae first ate the terminal bud, followed by the first open leaf and progressively devoured older leaves, as they grew (Fig. 2). They consumed all *P. suberosa* shoot parts, including tendrils, stipules and stem. In general, the terminal bud provided enough food to complete the first instar. During this instar some larvae ate part of the first open leaf as well. Leaf damage extended to the third, fourth and fifth open leaves during instars two, three and four, respectively (Fig. 2). There was considerable variation in fifth instar consumption rates. This variation in leaf consumption was expected, because leaves vary in size. About half the larvae required seven open leaves to complete larval development; however, some consumed up to ten leaves before pupation.

Larvae reared on intact *P. suberosa* shoots discriminated between the two leaf categories tested (Table 2). All instars preferred young over mature leaves in the leaf-disk choice test. Type of leaf age offered during fourth instar did not influence choice of larvae during fifth instar (one-tailed sign tests, $\alpha = 0.05$); they

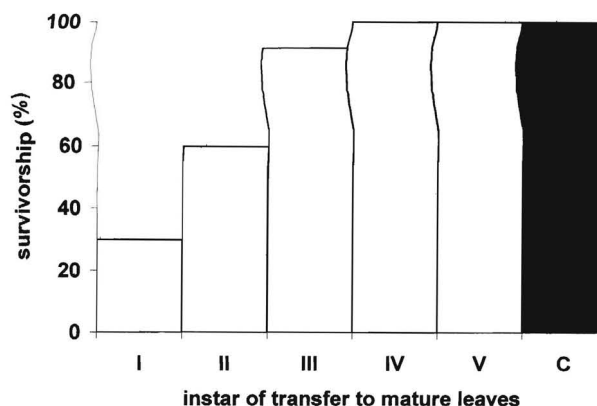


FIG. 3. *Heliconius erato* larval stage survivorship when transferred from young to mature leaves of *Passiflora suberosa* shoots. C, control = treatment 5.

preferred young over mature leaves when reared either on young ($p < 0.002$) or mature ($p < 0.005$) leaves of *P. suberosa*.

Leaf age affected *H. erato* survivorship during early instars (Fig. 3). There was a significant association between the age of transfer to mature leaves and percent survivorship (Spearman's rank correlation test, $Rho = 0.975$, $n = 5$, $p < 0.05$). When transferred to mature leaves during first and second instars only 30% and 60% of larvae respectively survived until pupation (Fig. 3). When transferred to mature leaves during third, fourth and fifth instars, larvae had similar survivorship to those kept on intact shoots (Fig. 3). Larval development rates were significantly longer when larvae were transferred to shoots containing only mature leaves as first or second instars, but there was no effect on later instars (Fig. 4).

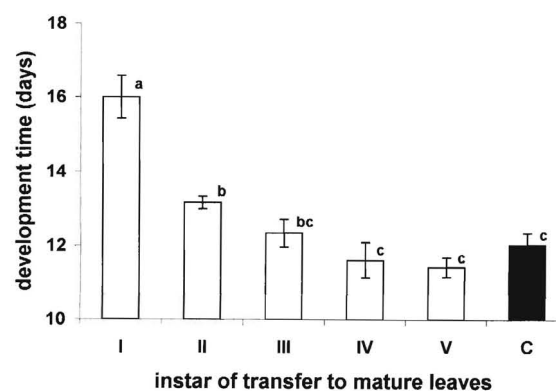


FIG. 4. *Heliconius erato* larval stage development time when transferred from young to mature leaves of *Passiflora suberosa* shoots. C control = treatment 5. Values followed by the same letter are not significantly different (Anova - log transformed data, $n = 48$, $p < 0.001$; Fisher's Protected Least Significant Difference multiple comparison tests, $p < 0.001$).

The size of adults that emerged from larvae transferred during fourth instar to cuttings containing mature leaves (36.97 ± 0.42 mm) was not significantly different from that of those kept feeding on young leaves (38.08 ± 0.37 mm) (unpaired, two-tailed *t*-test, $n = 36$, $p > 0.06$). Similarly, the size attained in the adult stage was not affected by transference imposed on all instars in the experiment designed to test effects of leaf age on larval performance (one-way Anova, $n = 35$, $p > 0.37$).

DISCUSSION

Our data confirmed field observations in that *H. erato phyllis* larvae feed continuously from the terminal bud (young tissues) to the basal portion (mature leaves) of *P. suberosa* shoots. Young tissues are preferred by all instars, and this preference is related to larval survivorship and development rates. As already pointed out, young larvae move to the terminal bud when placed on any mature leaf. Thus, larvae start feeding on the apical portion of the plant not simply because that is where the female lay the eggs. Larvae begin feeding on the apical portion of *P. suberosa* shoots because the corresponding tissues are more suitable for development of first larval instars. Larvae feed on a wider range of leaf ages in the later instars. A progressive loss in selectivity as larvae age has been found in some insects, however the underlying mechanisms for such an ontogenetic changes still not being clearly understood (Lewis & van Emden 1986). This ontogenetic change in feeding preference may be related to changes in nutrition, plant chemistry or mechanical barriers offered by young and mature *P. suberosa* leaves. Later instars may be better able to overcome defenses of older leaves and differences in food quality have most effect on the early instars; thus, the necessity to make the correct choices may be greatest for early instars (Reavey 1993).

The choice tests showed that later instar larvae prefer young leaves independent of the experience in the previous instar. Thus, they are expected to be found mostly on the youngest surviving portions of host-plants under field conditions. Results also indicated that the age of leaves consumed in a given instar does not influence choices made by larvae during subsequent instar. Even fifth instar larvae, which were comparatively less selective in relation to leaf age, showed preference for young leaves when fed mature leaves during fourth instar. Thus, *H. erato phyllis* larval preference could not be induced in relation to *P. suberosa* leaf age.

Induction of feeding preference, as a result of previous experience regarding particular plant species offered as larval food, has been demonstrated through choice tests performed with several lepidopterans

(Hanson 1983, Bernays & Chapman 1994; but see Bernays & Weiss 1996). Contrary to most of these lepidopterans that are polyphagous, *H. erato* is oligophagous, using a few *Passiflora* species as larval hosts in southern Brazil (Perico & Araújo 1991, Perico 1995). In an additional study carried out in our laboratory, Kerpel (1999) failed to show induction of larval feeding preference regarding the two preferred hosts (*Passiflora misera* and *P. suberosa*) of *H. erato phyllis* in Rio Grande do Sul State.

The data showed that *P. suberosa* leaf age strongly affects *H. erato phyllis* larval performance. Although it is not known to what degree mechanical and nutritional factors contribute to these effects, they may constitute the proximate cause for the maintenance of at least two egg-laying behaviors of *H. erato*. First, it may explain why females selectively oviposit on terminal portion of intact *P. suberosa* shoots (Lopes 1991, Mugrabi-Oliveira & Moreira 1996a); females that eventually oviposit on shoots lacking or with damaged terminal portion may be in disadvantage compared to those laying on intact shoots due to lower larval survivorship and perhaps inferior performance. Second, it may elucidate why females lay only isolated eggs on *P. suberosa* shoots (Mugrabi-Oliveira & Moreira 1996b). By avoiding multiple oviposition they may reduce intraspecific competition for the limited amount of leaves available on many host plants. *H. erato* larvae are cannibalistic, which is also an adaptation to host-plant size limitation (Brower 1997). Mugrabi-Oliveira and Moreira (1996a) found for a *P. suberosa* population of Viamão County, RS, that in more than half of *H. erato* eggs are laid on plants whose total leaf area is less than that required for larval development. Food shortage in the fifth larval instar has profound effects on survivorship and size attained in the adult stage (D. Rodrigues & G. R. P. Moreira unpubl. data).

Thus, we confirm the importance of variation in intraspecific attributes of *P. suberosa* plants, more precisely leaf age, in relation to preference and performance of *H. erato phyllis* larvae. Feeding preferences for young *Passiflora auriculata* tissues had already been demonstrated through choice experiments by Denno and Donnelly (1981) for larvae of *Heliconius sara* in Costa Rica. The physiological basis for such a feeding specialization in earlier instars remains undetermined. It is known that several chemical and physical traits of leaf tissues, such as pubescence, hardness, water content, nutrients and secondary metabolic compounds, vary according to age. It is also known that these leaf characteristics can play a major role in host-plant selection or performance of herbivorous insects (e.g., Scriber 1984, Slansky 1993, Bernays & Chapman 1994, Fernandes 1994), including flea bee-

ties that use *Passiflora* as host plants (Thomas 1987). Smiley and Wisdom (1985) found a significant correlation between leaf nitrogen content of several sympatric *Passiflora* species and larval growth rates of *Heliconius ismenius* and *Heliconius melpomene* in Costa Rica. They, however, failed to find any deleterious effects of potential toxins (including alkaloids, tannins and cyanogenic compounds) on larval growth rates and survivorship. Although not quantified precisely yet, there is a substantial increase in tissue toughness with advance in age in *P. suberosa* leaves. In consequence, ontogenetic changes in leaf age selection could also be associated with morphological constraints on *H. erato phyllis* feeding apparatus. Early instars of some grasshoppers and lepidopterans do not feed upon favored tissue or mature leaves because the mandibles are either not hard enough for effectively chewing, or their gape is not wide enough to grasp thick tissues (Bernays 1991).

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