REVISION OF THE EUPTYCHIINI (SATYRIDAE)

4. Pindis R. Felder

Lee D. Miller
Curator, Allyn Museum of Entomology

This paper is the fourth in a series of generic reviews (L. Miller, 1972, 1974, 1976) and another for which sufficient material exists in North American collections. The coverage of this genus at this time is governed more by convenience than by systematic relationship — it is hoped that the final paper in this series will be a compilation of the available data toward a systematically correct checklist of the species in the tribe and a phylogenetic interpretation of their interrelationships.

The present study is based upon 356 specimens from a cross section of the range of the single species that apparently belongs to Pindis. Additionally I have examined the type specimens or photographs thereof of the three names applied to that species. The sources of material are abbreviated in the same manner as in previous parts, and these acronyms are as given in L. Miller (1972: 2 and 1974: 1). Only newly cited references are given in the appended bibliography, but if the references cannot be found there, they may be in one of the previous parts of the revision.

There is only one species in Pindis, and it is rather variable. The possibility that all of the available names could be applied was examined in light of the plasticity of phenotypes, but the genitalia, which also vary slightly, do so without regard to phenotypic variations. The entire picture, then, is one of a single, variable species strongly affected by environmental conditions.

One other euptychiine has been placed in Pindis by Lewis (1973: 235; pl. 63, fig. 16), pellonia Godman and Salvin, but the male genitalia of pellonia have nothing in common with those of Pindis squamistriga, the type of the genus. In the case of "Euptychia pellonia" the gnathos arms are attached, as in Paramacera and Cylopsis (L. Miller, 1972 and 1974, respectively), whereas those of Pindis are free. The proper placement of "E." pellonia must await a later portion of the revision, and it will not be discussed further here.

The discussion that follows here will be longer than usual because of the degree of variability displayed by the single species involved.

Pindis R. Felder, 1869


The distinctness of Pindis from other euptychiines is attested to by its being one of
the half-dozen genera into which Weymer (1910-1911) placed all members of the tribe. This distinctiveness has not always been accepted, however, because Godman and Salvin (1879-1901) did not separate *P. squamistriga* from other "*Euptychia*", despite their usual predilection for generic splittings in other groups.

*Pindis* has no readily apparent close relatives in the tribe. Superficially it may be confused only with *Cyllopsis clinas* (Godman and Salvin), as indicated by L. Miller (1974: 95-96) in an earlier part of the revision. This resemblance is not a clue to relationship, however; perhaps a better case might be made with *P. squamistriga* and "*Taygetis*" *kerea* Butler, but even this relationship is not very close (see "Phylogenetic and Zoogeographic Considerations" section).

Since it displays the free gnathos arms, *Pindis* may be considered to be a "main line" euptychiine, but this in no way should be construed to mean that it is "typical". The wing shape, pattern and male genitalia (exclusive of the gnathos) are quite atypical in the group, and it stands as an aberrant member of the tribe, perhaps as much so as *Paramacera* or *Cyllopsis*. This genus, then, is another of the "old Mexican" ones and stands virtually alone within the Euptychiini.

It may be characterized as follows:

Eyes naked. Antenna about one-third length of forewing costa; club indistinct, occupying terminal third of antenna and inflated less than twice width of shaft. Palpus (Fig. 3) about half again length of head, semiporrect with tips slightly divergent; terminal segment just under half length of second; hairs of second segment long, greater than three times width of segment.

Thorax densely clothed with hairs dorsally and ventrally. ♂ foreleg (Fig. 4) slender, tibia slightly longer than femur and tarsus nearly as long as either, slender and pointed. ♀ foreleg (Fig. 5) slender and miniaturized (nearly as much so as that of ♂), with slender pentamerous tarsus spined on the second, third and fourth segments. Mid- and hindlegs short and slender, weakly spined on tibia and with well-developed tibial spurs.

Wing venation (Fig. 1) of a typical euptychiine pattern, but the wing shape is not (see discussion below). Forewing radial veins arising from cell in three branches; veins Rs and *M*₁ well separated at their origins; Sc and cubital stem noticeably, 2A only slightly, inflated at their bases, as shown; cells of both wings about half lengths of wings to ends of *M*₂; *C₁* of both wings somewhat nearer *M*₁ than *Cu₁*; hindwing humeral vein strongly developed and distinctly curved distad toward apex.

There is a large androconial patch (Fig 1) occupying the area in the cell of the forewing from the base of *Cu₁* to the origin of Rs, thence continuing outside the cell to *M*₂*C₁* (the most distal area included) and down to 2A, occupying the middle third of that cell. The individual scales are rather like those of the last three genera covered in the revision (L. Miller, 1972, 1974, 1976), differing from them chiefly in the rib structure (Figs. 40-42).

♂ genitalia (Figs. 12-14) as illustrated and characterized by the free gnathos arms, the heavy shieldlike tegumen and especially the heavy, downturned uncus. The valvae are relatively unornamented, and the penis is rather longer than that of most Euptychiini covered to date.

♀ genitalia (Fig. 15) also as illustrated, simple, lightly sclerotized (except in the sterigmal region) and only barely diagnostic.

To my knowledge nothing has been written concerning the early stages of *Pindis*. Such information would be of great interest, especially for determination of relationships with other genera within the tribe, relationships that are presently obscure at best.

The single species is highly polymorphic with respect to wing shape and color pattern, but the terminalia are far more constant. The wing shape varies between two extremes: The "normal", or *truncate-winged morph* (Figs. 1, 16-20, 28-29), is a basically smaller, more dull-colored insect with more uniformly and completely developed patterns of spots and lines; the *acute-winged morph* (Figs. 2, 22, 24-26, 32-39) is a redder insect with greater pattern above and a reduced, frequently heavily obscured pattern below, and it is a larger butterfly. Two of the available names were based upon the
truncate-winged morph, *squamistriga* R. Felder and *obnixa* Draudt, whereas *zabdi* (Butler) was based on a specimen approaching the acute-winged form. It is interesting to note with the acute-winged morph that the production of the forewing takes place in interspace $M_1$-$M_2$, rather than along either of the veins (Fig. 2).

Figures 1-5: *Pindis squamistriga* R. Felder. 1, δ venation; truncate-winged morph. 2, outline of outer margin of wing of acute-winged morph. 3, palpus. 4, δ foreleg. 5, η foreleg. Unless otherwise indicated, all specimens illustrated from Allyn Museum collection.
Pindis squamistriga R. Felder, 1869

All figures

*Pindis squamistriga* R. Felder, 1869: 475 ("Huahuapam" [perhaps Huajaapan de Leon, Oaxaca, Mexico]. Holotype in BM.

*Euptychia zabdi* Butler, 1869 [1869-1874]: 11 ("Chaetum" recte Choctum), Guatemala. Holotype in BM.

*Pindis obnixa* Draudt, 1931: 104 (Guerrero, Mexico; here designated). Lectotype in BM, here designated (see below).

In parts of its range *P. squamistriga* appears to be a highly variable species. Elsewhere the populations are remarkably monomorphic. This variability suggested that more than one species might be involved, and the male genitalia of the first few of each extreme morph examined appeared to be somewhat different than those of superficially unlike ones, but dissection of a series demonstrated that the genitalia, like the facies, varied slightly between individuals without apparent regard to other characters. In fact, even geographic subspeciation has not taken place in *P. squamistriga*, and all of the observed variation must be due to seasonal and/or climatic conditions. The redescription that follows, therefore, will be perhaps a bit longer than for previous euptychiines studied.

**Variations in wing shape:** The specimen used to illustrate the venation of the genus (Fig. 1) represents the most frequently encountered morph, what I earlier called the "truncate-winged morph". Other specimens range from this wing shape to the one illustrated in Fig. 2, the "acute-winged morph", in which the following modifications of the wing shape may be noted: 1) the forewing is produced, especially in M₂-M₃, with smaller projections as far costad as on R₁; 2) the crenulations at the ends of hindwing veins Cu₁, Cu₂, and 2A are far more pronounced than in the truncate-winged form; and 3) the forewing costa is somewhat more arched. These characters are by no means diagnostic, though, since they intergrade more or less independently from one extreme to the other. Some specimens are clearly intermediate, and these may well be flying with either or (rarely) both of the extremes. The shape as well as the size of the specimens is usually correlated with the brightness or dullness of the pattern and with development or reduction in the size and number of the hindwing ventral ocelli. The acute-winged morph is more frequent in specimens before me from southern Mexico, and at first I thought they might represent a distinct subspecies, but additional material from Guatemala and El Salvador proved to be indistinguishable from truncate-winged specimens from central Mexico. Apparently, then, these observed phenotypic differences are due to environmental vicissitudes and are not genetic in nature.

**Male:** Head, thorax and abdomen thickly clothed with warm brown dorsal and gray-brown ventral hairs. Antenna dark brown above, reddish-brown below; club reddish-brown on both surfaces, slightly darker at the tip. Palpus with dorsal brown hairs, elsewhere grayish-brown, slightly darker along ventral margin. Legs clothed with dense grayish hairs.

Wings above (truncate-winged morph) uniformly dull, dark brown; acute-winged morph slightly paler, lightest in distal third of forewing, this area delimited from inner two-thirds by a dark line roughly paralleling the end of the cell, then produced basally and continued to inner margin; a second submarginal dark brown line parallel to outer margin. Fringes tan, slightly reddened in acute-winged morph.

Under surface of forewing (truncate-winged morph) generally warm, dark brown with two darker marginal lines, a darker, slightly thickened submarginal line and a poorly developed extradiscal line from the costa to M₁ paralleling the end of the cell, then slightly inset and continued to 2A. In more acute-winged males the ground color is significantly reddened; the extradiscal band better developed, dark brown and extending to the inner margin; the marginal line missing altogether in some specimens, especially those that are heavily overscaled with gray distad; and in these specimens...
the submarginal line is obscured toward the costa. All intergradations may be noted between the extremes in long series.

Hindwing below (truncate-winged morph) usually gray-brown (occasionally slightly laved with reddish outside cell) with a narrow transcellular, slightly curved dark brown line, an irregular dark brown extradiscal band or line, produced distad in M₁-M₂, two marginal and one submarginal dark brown lines roughly following the outline of the wing margin and black ocelli from Rs-M₁ to Cu₁-2A between the extradiscal and submarginal lines (the ocellus in Rs-M₁ often absent, and any of the ocelli may be pupilled in white, most frequently those in M₁-M₂ and Cu₁-Cu₂); the entire surface heavily scrawled with gray-brown lines. The acute-winged morph is often much redder, the extradiscal and transcellular bands much more thickened, the marginal lines frequently absent (the submarginal one only faintly and irregularly indicated) and the ocelli are often absent (more commonly indicated by small black points of a few scales each); occasionally the ocellus in M₁-M₂ is indicated only by a small white patch with the other ocelli absent or very poorly developed. The fringes of both the fore- and hindwings below are tan-gray, somewhat redder in the acute-winged morph.

Figures 6-11: Type specimens. 6-7, *Pindis squamistriga* R. Felder, Holotype ♂ upper (6) and under (7) surfaces; MEXICO: “Huahauapam” (see text) (Allyn Museum photos 100477-C-1/2). 8-9, *Euptychia zabdi* Butler, Holotype ♂ upper (8) and under (9) surfaces; GUATEMALA: Choctum (Allyn Museum photos 091677-B-20/21). 10-11, *Pindis obnixa* Draudt, Lectotype ♂ (see text for designation) upper (10) and under (11) surfaces; MEXICO: GUERRERO (Allyn Museum photos 091677-B-26/27). All specimens in BM collection.
The males examined had forewing lengths of between 19.7 and 25.5 mm., averaging 22.4 mm. The truncate-winged males measured 19.7 to 24.9 mm., averaging 21.76 mm., whereas the most acute winged ones measured 21.8 to 25.5 mm., averaging 24.1 mm. The measurements of some representative populations are summarized in Table I.

The ♀ genitalia are as figured (Figs. 12-14) for the holotypes of *squamistriga* and *zabdi* and the lectotype of *obnixa*, respectively.

**Female:** The truncate-winged form varies little from its ♀, differing chiefly in the following: upper surface slightly laved with red in a few specimens; upper forewing with more pronounced extradiscal and submarginal bands delimiting a somewhat paler area between them; under surface just the same, but forewing slightly more likely to have a faint reddish shading in distal half. The acute-winged form is just the same as in the ♀, but the reddish color on both surfaces is more pronounced and the confused pattern of the hindwing below is even more so in this sex.

Lengths of forewings of the females at hand range from 20.8 to 28.3 mm., averaging 24.6 mm.; the acute-winged females range from 20.9 to 28.3 mm., averaging 25.7 mm., and the forewings of the truncate-winged ones range from 20.8 to 26.1 mm., averaging 24.3 mm. The forewing length measurements for females are summarized in Table I.

♀ genitalia as illustrated (Fig. 15): the sterigma is the only part that is strongly sclerotized, and the genitalia themselves are not especially characteristic.

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Figures 12-14: ♀ genitalia of type specimens of synonyms of *Pindis squamistriga* R. Felder. Specimens are the same ones figured in Figs. 6-11, and the same data apply. 12, *P. squamistriga*; slide M-1172 (Lee D. Miller). 13, *E. zabdi*; slide 13,167 (BMNH). 14, *P. obnixa*; slide 13,168 (BMNH). All specimens and slides in BM collection.
I have seen 356 specimens, 205 males and 151 females, from the following localities and collections. Not all of these have been used in the analyses that follow.

MEXICO: SINALOA: Loberas Summit, 5 mi. NE Potrerillos, 1820 m., viii, 1♀ (A).
JALISCO: viii, 2♂ 1♀ (A); 8.7 mi. W Magdalena, 1380 m., viii, 1♂ (A); Guadalajara, 2♂ 3♀ (AMNH); La Cumbre de Autlan, 3200-4200 ft., 6♂ 7♀ (AMNH).
MICHOCAN: vic. Pozos de Ixtlan, 1520 m., viii, 1♂ (A); El Sabino, nr. Uruapan, vii, 1♂ (A); Santa Lucrecia, ix, 2♂ (A). MEXICO: Tenancingo, iii, vi, 3♂ 1♀ (A); Malinalco, viii, 6♂ 2♀ (A). DISTRITO FEDERAL: Mexico, viii, 1♀ (A). HIDALGO: Jacala, 4500', vii, 2♀ (A). MORELOS: Cuernavaca, xi, 3♂ (A, BM, including "♀" Paralecotype of Pindis obnixa); Tepotzlán, 1650 m., vii-x, 7♂ 8♀ (A); 10 mi. S Cuernavaca, 1100 m., viii, 1♂ 3♀ (A); 5 mi. S Amacuzac, 900 m., viii, 2♂ 4♀ (A); 1 mi. S Xochicalco ruins, 1400 m., vii, 1♂ 2♀ (A); Yautépec, vii-viii, 5♂ 1♀ (A); Taxco, ix, 3♂ (JBS); Texalpa, ix, 1♂ 1♀ (JBS). GUERRERO: "Guererro", 1♂ (Lectotype of Pindis obnixa); Omitlente, x, xi, 2♂ (A); Acachiuzotla, vii, viii, 6♂ 7♀ (A); Chilpancingo, vi, ix, 2♂ 1♀ (AMNH, JBS); Huacapa Canyon, S of Petaquillas, 1020 m., viii, 1♀ (A); Tierra Colorada, vii, ix, 27♂ 3♀ (A); 2 mi. W Colotlpa, 1020 m., vii, 3♂ 1♀ (A); 2 mi. N of El Treintte, 220 m., ix, 3♂ (A); 5 mi. N of El Playon, ix, 2♀ (A). PUEBLA: Izucar de Matamoros, ix, 2♂ (A); "Matamoros" (same as preceding?), ix, 1♀ (AMNH); Caltepec, x, 1♂ (AMNH). VERACRUZ: Jalapa, 2♂ (CM); Presidio, vi, 1♂ (A). OAXACA: Huajapan de Leon, ix, 3♀ (A); Chimalapa, v, 1♀ (A); San José Pacifico, Mpio. Rio Hondo, 2400 m., xi, 14♂ 14♀ (A). NOT LOCATED: Almoloya, vi, 1♂ (A); "Huahuapam" (equal to Huajapan de Leon, Oaxaca), 1♂ (Holotype of Pindis squamistriga; BM); "Mexico", 2♂ (AMNH).

GUATEMALA: "Guatemala", 1♂ (CM); Chotchum (corrected from "Chaetum").

EL SALVADOR: Tamanique, 1000 m., vii, x, xi, 14♂ 2♀ (A).

NO LOCALITY: 1♂ 2♀ (A).

It was fortunate that when my wife was in England last autumn she was able to locate and photograph the type specimens of all three names presently carried in the synonymy of the present species. These specimens are figured in Figs. 6-11, and a brief discussion of them is here in order.

Pindis squamistriga (Figures 6, 7, Holotype 5; 12♂ genitalia of Holotype) was described by R. Felder from a single specimen captured by Hedemann at "Huahuapam". This locality is not on any of the maps I have consulted, but I suspect that it might have been a misspelling of Huajapan de Leon in Oaxaca, a locality from whence I have seen additional material. Such errors are common, even in modern

Figure 15. Pindis squamistriga R. Felder, ♀ genitalia; MEXICO: MEXICO: Tenancingo; slide M-3728 (Lee D. Miller).
material. The specimen, along with most of the Felders' material, passed to the British Museum (Natural History) via the Rothschild bequest. The Felder collection contained one other specimen of *squamistriga*, a ♂ taken considerably later at Cuernavaca, Morelos. Both specimens are of the truncate-winged morph and are fairly well ocellated below, as shown in the figures.

*Euptychia zabdi* (Figures 8, 9, Holotype ♂; 13, ♂ genitalia of Holotype) was based on a single ♂ in the Godman and Salvin collection from Choctum, Guatemala. Inadvertently Butler gave "Chaetum" as the type-locality, an error that was rectified by Godman and Salvin (1880 [1879-1901]: 81). As those authors state, *squamistriga* and *zabdi* were proposed within a few weeks of one another, and the only means by which we may be certain that the former name has precedence is that Butler (1869-1874: Corrections) states that Felder's name should be given precedence over his own. The Holotype ♂ is a large, reddish insect that approaches, but is not as extreme as, the "acute-winged morph" alluded to here. The hindwing maculation on the ventral surface is very dif-
ferent from *squamistriga*, but the ♂ genitalia, as shown, are almost identical.

*Pindis obnixa* (Figures 10, 11, Lectotype ♂; 14 ♂ genitalia of Lectotype) was described from "a pair" of specimens, both of which are now in the British Museum (Natural History) collection. Draudt’s "♀" type is actually a somewhat worn ♂ with the androconial patch obscured. It is from Cuernavaca, Morelos. Draudt’s ♂ type is in-

Indeed that and is from "Guerrero". I should have preferred to have made the Cuernavaca specimen the Lectotype, all other things being equal. But they are not equal: the Cuernavaca specimen was mislabelled as a ♀; it is in rather poor condition and the old "Cuernavaca" label could cover a multitude of places in which the insect flies. Accordingly, then, I am designating the other specimen (Draudt's original ♂ type) as the Lectotype of *Pindis obnixa*. It bears the following labels: 1) a round, red bordered BM "Type" label; 2) a label with the printed number "54"; 3) a black bordered label stating "Mexico/ GUERRERO / ix.12" (Italicized entries = handwritten); 4) a partly printed, partly handwritten pinkish label, "Type/ Pindis/ obnixa/ ♂ Draudt"; and 5) a printed label, "Brit. Mus./ 1934-239" referring to the BM accession. To this I have added a red label hand printed in black, "Lectotype ♂/ Pindis obnixa/ Draudt / designated by / Lee D. Miller, 1978". The other syntype is a Paralectotype and will be labelled accordingly. The types of *obnixa* are very little different superficially from the type of *squamistriga* (perhaps a bit more heavily ocellated), both belonging to the truncate-winged morph.

The androconial scales (Figs. 40-42) are not appreciably different from those of some other Euptychiini, but the ribbing structure is quite different. Just what taxonomic significance to attach to these scales must await further studies in the tribe: the configurations are presented here simply for comparison purposes.

*P. squamistriga* is a species of mesic woodland environments in the Mexican localities in which I have encountered it. It behaves very much like other open woods euptychiines, but perhaps its flight is a bit more erratic than others. The adults will land on the ground with the wings about half open and bask in dappled sunlight. When approached, however, they will snap the wings together and heel over slightly to one side, thus effectively cutting down on their visibility by minimizing shadows. When disturbed the flight is rather rapid (for one of the Euptychiini) and very jerky; their habit of darting in and out of the brush makes them difficult to capture.

Variation: A series of specimens of either sex will yield specimens that vary greatly in under surface facies (Figs. 16-39). The specimens that are like the type of *squamistriga* are heavily ocellated on the hindwing, and the ground color is a rather uniform gray-brown. From that extreme one may observe specimens with an almost unmarked grayish ventral hindwing (Fig. 31, for example), others with strong reddish flush and either patterned (Fig. 34) or unpatterned (Fig. 36). The ocelli on these forms are usually reduced or absent, but a few specimens (Fig. 20) will show development of the ocelli rivaling that of the truncate-winged morph.

All or some of the ocelli may be pupilled in white (Fig. 28), as in the type of *squamistriga* (Fig. 7), but in other specimens all ocelli are blind (Fig. 29, for example). In a very few specimens the ocelli, especially the anterior ones, may be entirely represented by white blotches with no black irides (Fig. 27 is an extreme example).

The dorsal surface is relatively invariable, individuals differing chiefly in the amount or lack of reddish suffusion. The submarginal and extradiscal lines of the under

forewing are usually better developed in the *zabdi*-type morph, except where the costa is heavily overscaled with gray.

The wing shape differences between the various morphs have been discussed earlier, and it suffices to say that intergrades between the extremes are not uncommonly found flying with examples of other morphs. Similarly, size differentials exist between individuals, and as shown in Table I, a case could be made for separating some populations from one another. Taking into consideration the presence of several wing-shape and pattern morphs within a single population, however, it was determined that the observed size differences were more likely to be environmentally controlled (foodplant quality, etc.) than genetically related. Hence, the decision not to subdivide *P. squamistriga* into geographic races.

I do not expect *P. squamistriga* to be taken much further south than the central El Salvador locality recorded herein. There is a possibility that it might be discovered in northwestern Honduras, but the fact that it has not been collected in southern Guatemala or southeastern El Salvador suggests that the Tamanique locality is about the furthest possible southern extent of this species. Furthermore, it is unlikely that *squamistriga* will be found in southwestern New Mexico or southeastern Arizona: both of these areas have been collected rather extensively without uncovering the present insect. The fact that it was taken on Loberas Summit, Sinaloa, in company of such Arizona residents as *Neophasia terlooti* (Behr) and *Pyrrhopyge araxes arizonae* Godman and Salvin at least suggests the possibility (no matter how remote) that *squamistriga* might occur in the mountains of southern Arizona.

**PYLOGENETIC AND ZOOGEOGRAPHIC CONSIDERATIONS**

No other euptuchiine closely corresponds with *P. squamistriga* superficially or in genitalic configuration. “*Taygetis*” *kerea* and *Megaeuptychia antonoe* (Westwood) have somewhat similar genitalia, but even here the relationship is not very close. It appears, therefore, that *squamistriga* is another of the “old Mexican” species that stands apart from its relatives, thus signifying long isolation. Historical geography gives us evidence that the western part of Mexico was an island through much of the Tertiary, and this isolation at about the right time gives a plausible explanation for such a divergent genus as *Pindis*. Again, this faunal area has produced many strangely evolved butterflies, *Baronia brevicornis* Salvin (Papilionidae), *Prestonia clarki* Schaus (Pieridae) and *Phanus rima* Evans (Hesperiidae) being only examples.

It appears then that the ancestor of *Pindis* reached this Guerrero-Oaxaca “refugium” long ago and developed *in situ*. This progenitor of *Pindis* was not the same as the ancestor of *Cyllopsis* or *Paramacera*, since both of those genera have gnathos im-

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</table>
movably placed, rather than free as in the present genus. The western Mexican area must have supported a moderately well developed butterfly fauna during this time, much of which has survived (doubtless in modified form) to the present. *Pindis* spread from this ancestral home further than did many other members of the "old Mexican" fauna, but it did not move as far north as did *Paramacera*, concentrating its dispersal in areas further to the south.

While little of substance can be said about the relationship between *Pindis* and other Euptychiini, it is hoped that these will become clearer as the study progresses.

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LITERATURE CITED

If a paper is not listed herein, reference to it will be found in L. Miller (1972, 1974, 1976).


Figure 43: distribution of *Pindis squamistriga* R. Felder.