

**THE PROBLEM OF THE *LESTES PALLIDUS* GROUP
(ZYGOPTERA: LESTIDAE)**

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The three related species of *Lestes*, *pallidus* Rambur, 1842, *ochraceus* Selys, 1862, and *ictericus* Gerstäcker, 1869, were inadequately described from single specimens, all of which lacked most of the abdomen, and the appendages most commonly used in separating species. Attempts by later authors to distinguish them by colour and pattern have only led to confusion. The species have now been reconsidered in the light of field observations on colour changes during maturation, and distinguishing characters looked for in the shape and venation of the wings. The original type-specimens have been reexamined in hopes of establishing with which of the species occurring in the field they correspond.

INTRODUCTION

The problem of *Lestes pallidus* is, – to put it briefly, – which species is which. The first three African species of this group to be described, *pallidus* Rambur 1842, *ochraceus* Selys 1862, and *ictericus* Gerstäcker 1869, were described inadequately, from single specimens; the first from a female, the others from males, and all with the posterior half of the abdomen either in a fragmentary condition, or else totally lacking. The original descriptions based the differences mainly on colour and markings, which vary greatly with the state of maturity of the specimens – as well as with post-mortem changes: – and most later redescrptions (some of which are extremely good) are based on specimens other than the original types, and not necessarily of the same species.

In addition to these three, McLACHLAN (1895) described *unicolor* from Madagascar, which is a valid species. But most or all species of this group described from Africa during the present century are probably new names for

old species, based on specimens at different stages of development from the types, *somalicus* Förster 1906; *chromatus*, *cineraceus*, *jacobi*, and *radiatus* Martin 1910; *wahlbergi* Ris 1921; *stigmatus* Navas 1924; *geminatus* and *disarmatus* Fraser 1951 and 1961. RIS partially revised the group (1908, 1912, 1921) and redescribed and figured what he considered to be *ictericus* and *ochraceus*. FRASER (1950) decided that both these were forms of *pallidus*, probably ecological variants, thus leading to the tiresomely confusing names *L. pallidus ictericus* and *L. pallidus ochraceus*.

My approach to this problem has been fourfold.

(1) First, I reviewed my field observations made during 14 years residence in Nigeria to see, — as far as available data could show, — how the pattern of colour and markings changed during the course of maturation, in these and similar species.

(2) Next I looked to see how many of these species were to be found, first in Nigeria where I had first-hand experience, then from Africa as a whole, from specimens in the British Museum and from any private collections from which I could borrow material, and then those described in the literature; and familiarised myself with the appendages of the males, and the ovipositor valves of the corresponding females.

(3) Then I examined all these specimens for characters other than the terminalia by which the species could be separated, mainly those of the venation, measurements, and shape of the wings.

(4) Finally, when I felt reasonably at home among the different species, I borrowed the types of *pallidus*, *ochraceus*, and *ictericus* from the Brussels and Berlin Museums, by the kindness and courtesy of Drs Demoulin and Günther, to see whether in the light of these wing characters I could say with which of the species I had recognised in the field and elsewhere, these original types corresponded, and so decide which name was correctly to be applied to which species.

FIELD OBSERVATIONS ON COLOUR CHANGE DURING MATURATION

The first two species of *Lestes* that I found in Nigeria were *plagiatus* and *virgatus*. The former seemed unlike all the other species I studied in that as it usually bred in flowing streams, and only occasionally in shallow ponds, it could — and did — emerge at any time of the year, and at no time was the whole population at any single stage of development. But *virgatus*, and as far as I could see all other Nigerian species of *Lestes*, bred almost entirely in shallow temporary ponds in the rainy season, completing the larval stages in about two months, and living as adults through the long dry winter.

This species was very common in Vom where I was stationed, on the central plateau of Northern Nigeria, in the Guinea Savannah belt, at a height of about

1500 metres (9°43'N, 8°47'E). It could be found abundantly in a habitat which I found most productive, although possibly neglected by many Odonatologists, dry grass and ground herbage, especially under the shade of trees. It is well-known that adults when they emerge, fly away from water for a period while they become sexually mature, – usually about two weeks in temperate climates, – and then return to the water to breed. But in tropical climates with long, hot, dry seasons, this maturation period may be prolonged for many months, thereby delaying sexual maturity until water is again available for larval development. During this period an abundant dragonfly fauna was to be found over shaded ground herbage, with immature colours and markings, both sexes present in approximately equal numbers, and showing no signs of sexual activity. *Lestes virgatus*, *L. ochraceus*, *Ceriagrion moorei*, and *Pseudagrion glaucescens* were the commonest species found in this habitat. The mature colours of all these species were so different from what they had been during the dry season, that I completely failed to recognise them the first time I met them, although extremely familiar with them in the colours they had worn during the long dry months.

The next two *Lestes* that I met were very similar in appearance and it took me some time to satisfy myself that they were separate species, especially as at first I only had a female of one and males of the other. The first was from dry grass under trees in November, and the others from a marshy pool in April. But when I found more of the former the following November, of both sexes, I was able to find a slight but definite difference in the shape of the male appendages, and with assistance from Miss Longfield was able to recognise them as the two species which Ris had redescribed as *ochraceus* and *ictericus*, and for the time being I will use Ris's names for them. I became very familiar with *ochraceus* in its immature colours away from water during the winter months, but unfortunately I never found it in its sexual stage. On the other hand, I only found *ictericus* at water, apart from one of each sex which I found flying over a stubble field in the middle of the dry season, when the general colour and markings were exactly the same as those of an *ochraceus* found in the same place and at the same time. These were the only specimens of the two species taken by myself at the same stage of development. I was later sent a packet of specimens from Nigeria for identification containing a male *ochraceus* and a female *ictericus* from the same general locality on the same day in December, (the nature of the habitat was unfortunately not specified, but must presumably have been over dried grass). These looked so exactly alike that my correspondent had obviously thought them the same species. The first time that I saw *ochraceus* fully mature was when a pair were sent to me from the Ivory Coast, very dark, and so different in appearance from the species as I knew it that for some time I failed to recognise it. Thus, although I have very little material at comparable stages of development to provide evidence, the general probability -- supported by what

evidence there is – seems to be that both species pass through the same colour changes during their development, only differing by venation and the morphology of the appendages, and probably having a similar annual life cycle.

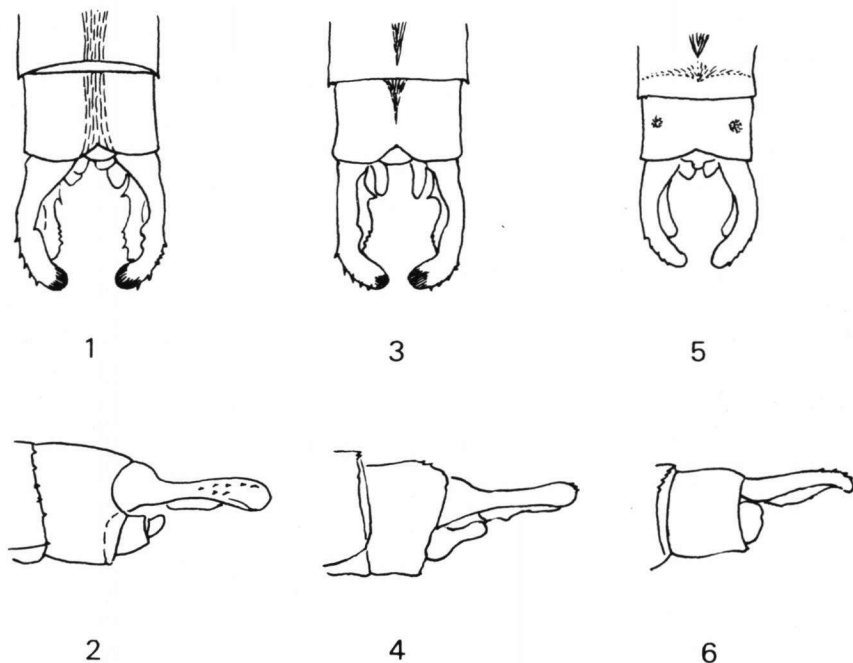
I found the species I called *ictericus* at various times during the rainy summer months, though only from a limited number of localities. The second time was by a pond 30 Km away from the first, one July. These were rather darker than the April specimens, which had only been distinguishable from dry season *ochraceus* by morphology, by generally more mature colours, and a slight pruinescence at the wing-bases. The species was found at a third pond in the extreme North of Nigeria in the last August before I left, and here they were so dark that at first I failed to recognise them as *ictericus*.

I found two females of a third species of this group one August, flying among reeds and other emergent vegetation in a flooded pool beside a river. I left Nigeria without having been able to identify these or find any further specimens, but fortunately Dr and Mrs Parr found both sexes near Zaria in North Nigeria, and this enabled me to recognise them as the species described by Fraser as "*L. disarmatus*" in PINHEY's (1961) "Survey of the Dragonflies of Eastern Africa". These were a darkish unicolorous brown, except that the last segment was very pale, almost white. In general, the appearance was intermediate between the other two species. And the wings were conspicuously rounded at the tips. I was recently sent a mature male of this species, taken last August from West Nigeria, with dark body colours, and the wings somewhat infuscated. And a few weeks ago, sorting out some boxes of papered material to see if I had any further *ochraceus*, I found an immature female "*disarmatus*" from a typical dry grass habitat one January that I had – even after ten years experience of *ochraceus* – mistaken for that species. The short pterostigma must have caught my attention, for I had made a note on the packet "verify", but had forgotten to do so. So this specimen suggests that the immature stage of "*disarmatus*" is exactly similar in appearance to those of Ris's "*ictericus*" and *ochraceus*.

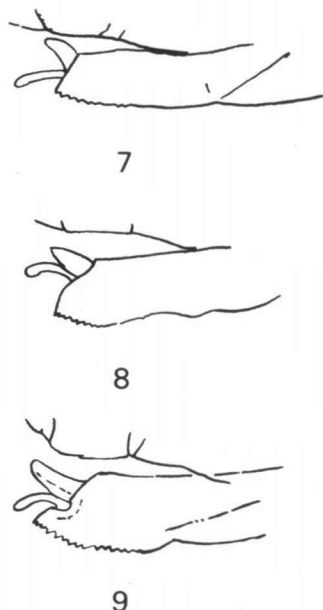
Other species of *Lestes* that I found in Nigeria, not belonging to this group, seemed to fit into the same sort of annual life cycle; *tridens*, which I found over ponds (May-August); *pinheyi*, which I only knew from its immature stages over grass (November-May); and *simulans*, which I knew both from ponds (oviposition from April to October, but the extremes were noted from the South, where the rainy season is much longer), and from its immature stages (November-April). Dr and Mrs Parr have found another species, *uncifer*, related to *pinheyi*, in its mature form at water, during the rains, near Zaria. These observations all tend to the conclusion that these species (with the exception of *L. plagiatus*) all spend the dry winter months, October to March, or even longer, in a prolonged immature stage away from water, with colour and pattern quite different from the sexually mature phase found later at water during the rains. So that to base descriptions of new species on colour and pattern can only lead to confusion.

DISTINCTIVE CHARACTERS OF ♂ AND ♀ TERMINALIA OF THE SPECIES OF *PALLIDUS* GROUP

In all the material I have examined in my own and other collections (over 150 specimens examined in detail, and many others more casually). I have only found these three species of the *pallidus* group anywhere from Continental Africa, Ris's *ictericus* and *ochraceus*, and Fraser's *disarmatus*. The three species were clearly distinguishable by the degree of curvature of the superior appendages of the male (Figs. 1, 3, 5), the length of the inferiors (Figs. 2, 4, 6), and the shape of the ovipositor valves of the female (Figs. 7-9). But when, — as in the



Figs. 1-6. Appendages of male *Lestes* spp., dorsal and left lateral views: (1-2) "*L. ictericus*" sensu Ris (= *L. pallidus* Rambur); — (3-4) "*L. ochraceus*" sensu Ris (= *L. ochraceus* Selys); — (5-6) "*L. disarmatus*" Fraser (= *L. ictericus* Gerstäcker, nec Ris & auct.).



case of the types, — these vital structures are missing, fortunately there are enough other characters to say to which of the three species a specimen belongs. Ignoring colour and markings, which we have seen to be so variable and age-dependent, and as FRASER (1950) points out, very liable to be masked by adventitious markings and colour changes arising post-mortem, I shall concentrate on morphological details, which will have to be mainly venational. I have left the penis until later studies, as no Museum is likely to wish their historic types to be put at risk by the dissection of this organ.

Figs. 7-9. Ovipositor and valves of female *Lestes* spp., right lateral: (7) "*L. ictericus*" sensu Ris (= *L. pallidus* Rambur); — (8) "*L. ochraceus*" sensu Ris (= *L. ochraceus* Selys); — (9) "*L. disarmatus*" Fraser (= *L. ictericus* Gerstacker, nec Ris & auct.).

DISTINCTIVE VENATIONAL CHARACTERS

Selys, comparing the type of his *ochraceus* with that of Rambur's *pallidus* mentions the post-nodal cross-veins, 9-10 in the forewing of *pallidus* and 12-13 in *ochraceus*, and the row of cells two below the pterostigma ("secteur ultranodale") becoming double two cells before the pterostigma in *pallidus* and four cells before in *ochraceus*. Both these differences are useful guides to general tendencies, but not absolute distinctions. Few of my supposed *ochraceus* have as many as four cells doubled, and one single wing had as few as 1½, but taken by and large there was a definitely higher number in *ochraceus* than in what I had been calling "*ictericus*"; similarly with the number of post-nodals (see histograms, Fig. 10). Selys mentions two dark spots on the ventral surface of the thorax in *ochraceus* just behind the base of the hindlegs, and these were invariably present in my own *ochraceus* but not in any of my Nigerian "*ictericus*". However Ris mentions them as sometimes present in the latter species, and looking at specimens from all over Africa I found them present as often as not, though seldom as large or as obvious as in *ochraceus* where they are invariably present. Selys also mentions that the venation is closer in the distal and posterior portion of the wings in *ochraceus*, and this also seems to be borne out, but it is difficult to find a simple way of measuring this. I had also noticed when I first started to compare the two species that the pterostigma was slightly larger in

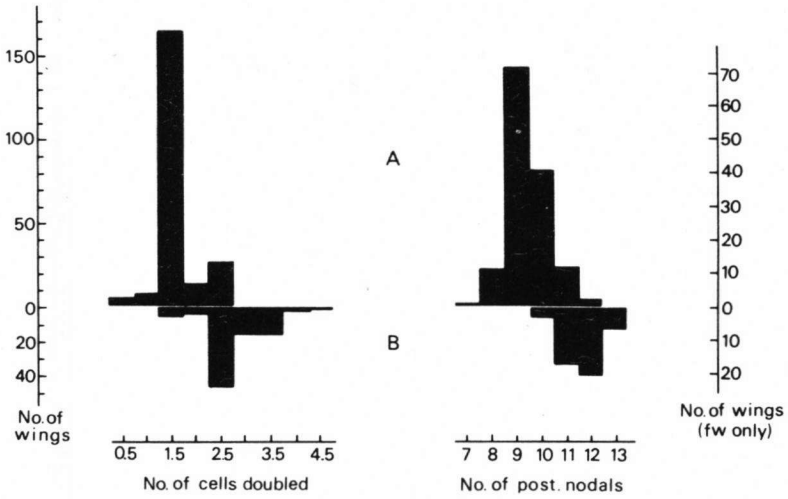


Fig. 10. Histograms of distribution of number of cells doubled in the ultranodal sector, and of numbers of forewing postnodals: A: "*L. ictericus*" sensu Ris (= *L. pallidus* Rambur); – B: "*L. ochraceus*" sensu Ris (= *L. ochraceus* Selys).

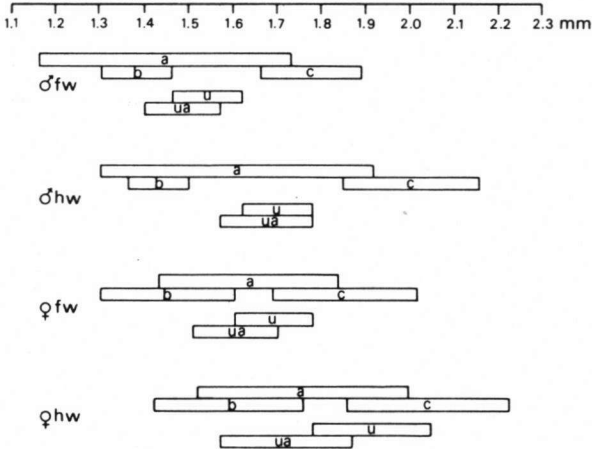


Fig. 11. Histograms of range of pterostigma lengths in *Lestes* spp., broken down according to sex, and to whether fore- or hindwing: a: "*L. ictericus*" sensu Ris (= *L. pallidus* Rambur); – b: "*L. disarmatus*" Fraser (= *L. ictericus* Gerstäcker, nec auct.); – c: "*L. ochraceus*" sensu Ris (= *L. ochraceus* Selys); – u: *L. unicolor unicolor* McLachlan (Madagascar); – ua: *L. unicolor aldbrensis* Blackman & Pinhey (other islands).

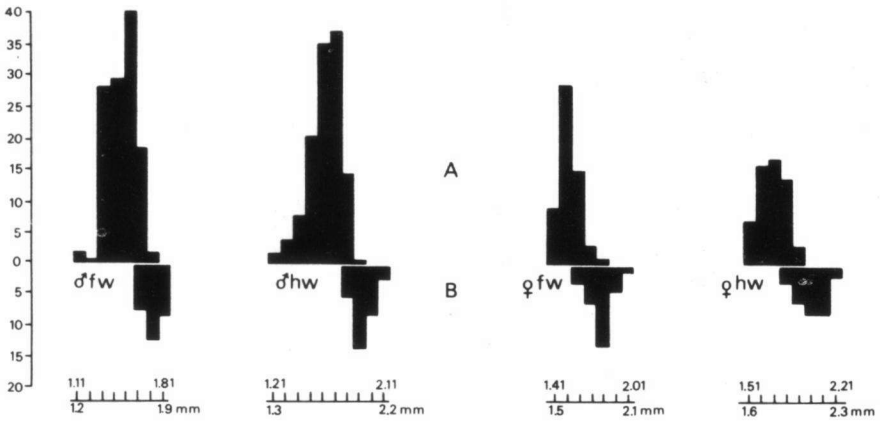
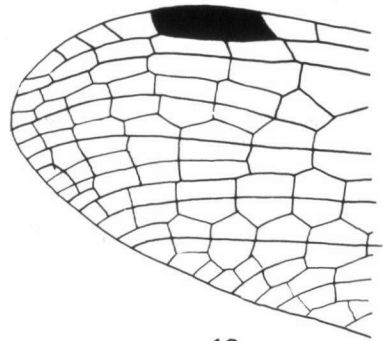
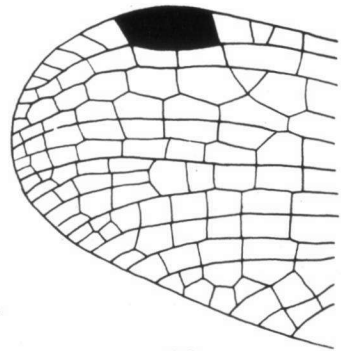


Fig. 12. Histograms of distribution of pterostigma lengths, according to sex and to whether fore- or hindwing: A: "*L. ictericus*" sensu Ris (= *L. pallidus* Rambur); – B: "*L. ochraceus*" sensu Ris (= *L. ochraceus* Selys).

ochraceus, and this proved to be the most helpful single character for separation. There is considerable overlap between the measurements of this (taken as the length along the costal margin, including the two cross-veins bounding it, using an eyepiece micrometer) in Ris's "*ictericus*" and *ochraceus*, but if the pterostigma is measured separately, forewing and hindwing, male and female, and like compared with like, there is then very little overlap in the forewings of the same sex, and scarcely any at all in the hindwings (histograms, Figs. 11-12). Where the length of the pterostigma is on the borderline in one wing, that on the opposite side will often give a more clear-cut indication; and true borderline cases can be separated by the number of post-nodals, and by the number of cells doubled before the



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Figs. 13-14. Tip of forewing: (13) "*L. ictericus*" sensu Ris (= *L. pallidus* Rambur); – (14) "*L. disarmatus*" Fraser (= *L. ictericus* Gerstaecker, nec auct.).

pterostigma. By such means I hoped to be able to say to which of these available species the various types belonged. The third species, which Fraser called *disarmatus*, has a pterostigma that falls entirely within the range of Ris's "*ictericus*", but it can easily be distinguished by the border of the wing being much more rounded (Figs. 13-14). In the number of post-nodals and doubled cells it is like *ochraceus*.

We thus have three species, widespread through Continental Africa, which can be clearly distinguished by their morphology regardless of sex, by the male appendages or by the ovipositors; and, even if these features are missing, by a combination of the length of the pterostigma and the shape of the wing-margins, with additional presumptive support given by the number of post-nodals and the cells doubled in the ultranodal sector.

THE TYPE SPECIMENS

At this stage, to see what these species really looked like, and whether the names I had hitherto been using were correctly applied, I asked Brussels and Berlin if I might borrow the types for examination. These promptly arrived, and I was not entirely suprised to find that of *pallidus* was the species which Ris had called "*ictericus*". The specimen is in poor condition, and lacks most of the abdomen, but the end segments – though rather incomplete – have been glued to the pin which has been inserted to support the abdomen, and include ovipositor valves of what I had been calling the "*ictericus*" pattern, following Ris's definition of that species. The pterostigma measured 1.60 mm in the forewing and 1.80 mm in the hind, well within the range of that species, and too short for *ochraceus*. It has the typical 9-10 post-nodals, cells in the ultranodal sector doubled $1\frac{1}{2}$ cells before the pterostigma, and the wingtips of the normal rather pointed shape. So what Ris, and all those of us who followed him, have been calling *ictericus* should have been called *pallidus*, – as Fraser said, though for the wrong reasons.

The type of *ochraceus*, which Ris had examined, was – as expected – the species he redescribed under that name in 1921. The pterostigma in the forewing was very slightly shorter than any I had examined, and in the hindwing only slightly longer than the shortest, but it was at the extreme end of the range of the true *pallidus*, reached only by a few which were exceptionally long in the pterostigma (in 62 male *pallidus* examined, only one had the pterostigma as long in both hindwings, and another in one hindwing only). The number of post-nodals and doubled cells was well out of the range of *pallidus*, and there can be no doubt of the identity of Ris's *ochraceus* with Selys's type.

I was expecting Gerstäcker's *ictericus* to be the species redescribed under this name by Ris, and thus a synonym of *pallidus*. So when the type arrived from Berlin, I was amazed to find that it had the rounded wing-margins of Fraser's

"*disarmatus*", pterostigma in the lower part of the range of what we must now call *pallidus*, but with 12 postnodals (as in Fraser's type), and more cells doubled than is usual in *pallidus*. So Gerstäcker's *ictericus* is after all a perfectly good species, easy to recognise, and Fraser's "*disarmatus*" is merely a synonym. Gerstäcker's words "a *Lest. pallida* Ramb. et *ochracea* Selys corpore unicolore alisque brevioribus discedens" now take on a new colour. I had always thought the mention of shorter wings than the other species referred merely to a matter of a few millimetres. But it may well refer to the conspicuous way in which the wings are rounded off shortly instead of extending out to a longer point as in the other species.

CONCLUSION

The three original species described from Africa in the "*pallidus* group" have thus all been vindicated, and as originally described are quite distinct from each other. McLachlan's *L. unicolor* from Madagascar, with its subspecies *aldabrensis* Blackman & Pinhey from other islands in the Indian Ocean, now recorded from Aldabra, Cosmoledo, and Zanzibar, is a distinct species though closely related to *ochraceus* (mainland records are almost certainly misidentified, as are Island records of *ochraceus*). But most, if not all, of the other African species of this group described since are probably merely synonyms of one or other of the three original species which we have been discussing. One remaining point to consider is the status of Rambur's type. Various authors starting with SELYS (1862) have commented on the fact that the species was originally described from the Cape, but that the type carries a label "Senegal". Selys did not indicate whether he thought this merely a careless mistake (either in the description or in the labelling), or whether he thought both correct and the specimen not the one originally described. So I propose that we accept the former alternative, which is not only convenient, but also probably correct, for the position of the dark markings on the thorax, and what remains of those on the abdomen, fit the details of the original description exactly. If on the other hand it is considered that the specimen is not the original one, in which case the latter must be irrevocably lost, then let us regard the present specimen as a neotype – even though it is not from the type-locality. It has been accepted as the type for well over a hundred years, and its acceptance raises no problems as to its identity; so to leave it without further challenge is in the interests of stability of nomenclature.

Finally, let us salute the workers of the previous century, who without the sophisticated criteria of our age, nevertheless when faced with mutilated single specimens of the three species were able to realise that all three were clearly distinct. We who follow have confused them with each other, lumped them, split them, and described new species unnecessarily, while they – with unerring instinct – recognised the truth when they saw it!

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