TWO NEW SUBSPECIES OF *PHACOPS RANA* [TRILOBITA] FROM THE MIDDLE DEVONIAN OF NORTH-WEST AFRICA

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ABSTRACT. *Phacops rana africanus* subsp. nov. and *P. rana tindoufensis* subsp. nov. are described from the Middle Devonian of North-West Africa. They are considered to be close to *P. rana milleri* Stewart and *P. rana crassituberculata* Stumm of North America. An origin for *P. rana* in the European and North African *P. schloteimi* (s.l.) group is postulated. Migration of forms between the two areas is necessary to explain the distribution pattern of *P. rana*, and routes between North-West Africa and North America are examined with reference to the contemporary positions of the continents.

DURING an investigation into the phacopids of North-West Africa by one of us (C. J. B.), two unusual forms were noted from the Middle Devonian of the Tindouf Basin of Spanish Sahara, northern Mauritania, and Morocco (see Map, text-fig. 1). These forms have been described in literature, and informally identified in collections, as *Phacops schlotheimi* (s.l.) and *P. fecundus degener* Barrande. The present authors believe them to belong among the subspecies of *P. rana* (Green 1832). The two forms are close to *P. rana milleri* Stewart and *P. rana crassituberculata* Stumm of the Middle Devonian of North America, and two new subspecies, *P. rana africanus* and *P. rana tindoufensis* are erected for their reception.

This identification of North-West African forms with a group not hitherto recognized outside North America and eastern Asia has raised a number of problems. Firstly, the problem of the origin of *P. rana*. In view of the close similarity with the *P. schlotheimi* (s.l.) group, especially in details of eye morphology, the authors believe that the latter and *P. rana* are closely related. This similarity, coupled with the new discoveries and the fact that there is no close relation to *P. rana* in the Lower Devonian of the Americas, has led us to explore the possibilities of a relationship between *P. rana* and European phacopid lineages. Secondly, a possible phacopid migration into North America raises the general problem of routes. The work is based entirely on museum material. French usage is followed for Arabic place names.

NOTES ON MORPHOLOGICAL AND OTHER TERMS USED

In this paper the terms used to describe the phacopid exoskeleton follow the usage of the *Treatise on Invertebrate Palaeontology*, Pt. **O**, Arthropoda 1 (R. C. Moore, ed. 1959), except in the following cases:

Eye socle. This is the curb-like ridge supporting the visual surface of the eye, in the sense of Shaw and Ormiston (1964, p. 1002).

Group. In this paper the '*Phacops schlotheimi* group' refers to subspecies of *P. schlotheimi* and also to species morphologically close to it and demonstrably separate from other European and African species of the genus *Phacops*. The group in this sense is an informal device for assembling morphologically similar species and subspecies without any rigid taxonomic commitment (see Burton 1972 for morphological details and discussion).

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Intercalating ring. This is used instead of the term 'preoccipital glabellar lobe' of the Treatise (p. 125), since in most phacopids this character is a definite ring, not simply an area of the glabella. The intercalating ring corresponds to the 'Zwischenring' of Richter (1926, p. 126) and the 'Anneau Intercalaire' of Barrande (1852, p. 503).

The intercalating furrow is that furrow anterior to the ring (glabellar furrow 1p).

Interlensar sclera (Clarke 1889). That part of the visual surface which lies between the schizochroal lenses and is not covered by cornea.

Palpebral lobe and *fixigenal eye stem.* The term palpebral lobe is reserved for the area above the visual surface. The term fixigenal eye stem is reserved for the discrete ridge separated from the palpebral lobe by the palpebral furrow and running posteriorly from it.

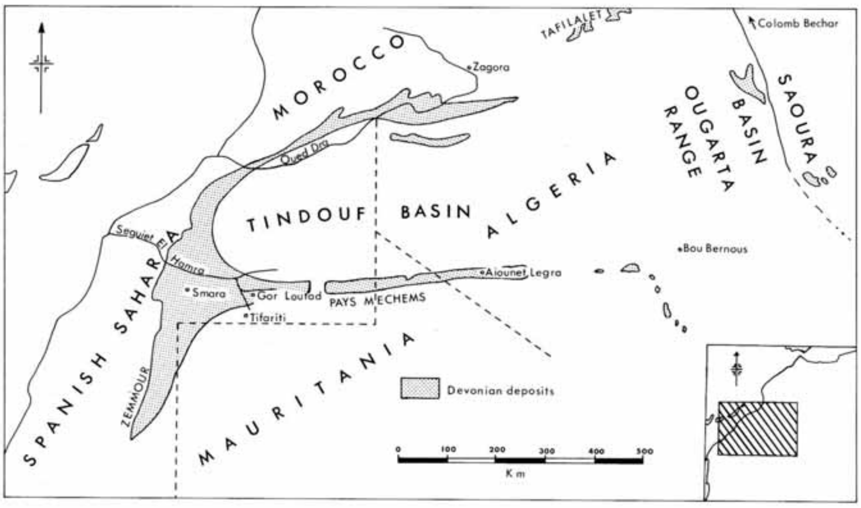
Rear-eye ridge. A term used for the ridge which is a continuation, in a lateral direction parallel to the posterior cephalic margin, of the fixigenal eye stem. The ridge is bounded distally by the facial suture. The term rear-eye ridge is not a synonym of the term 'postocular ridge' used in the Treatise (p. 124).

Abbreviations. The following abbreviations are used:

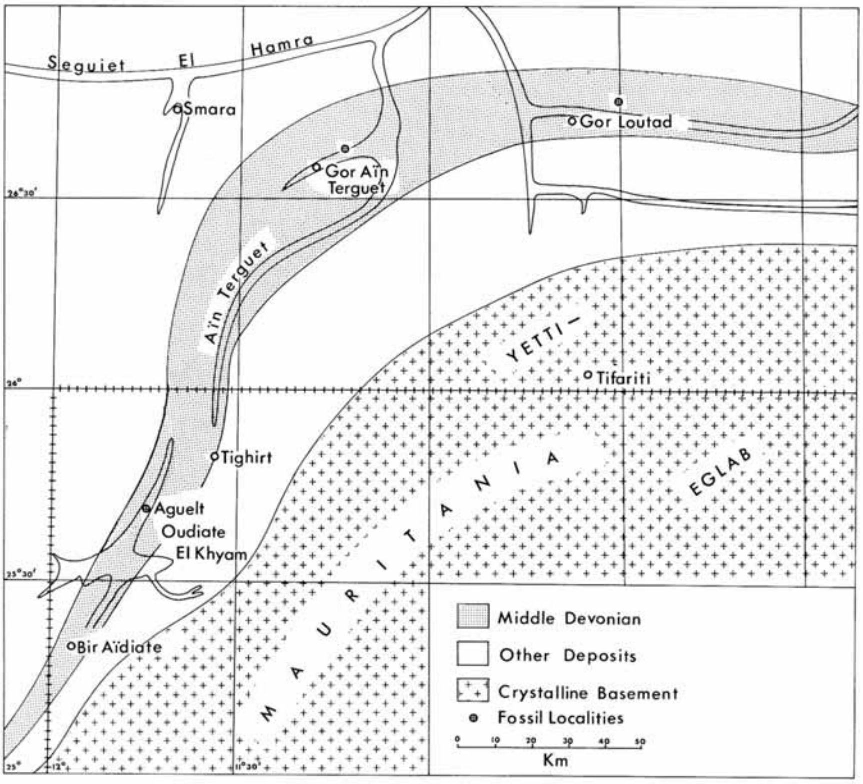
AMNH—The American Museum of Natural History;
BMNH—The British Museum (Natural History), London;
ULL—L'Université Libre de Lille, France;
USNM—National Museum of Natural History (formerly United States National Museum);
SUI—the State University of Iowa.

STRATIGRAPHY AND PALAEOGEOGRAPHY

The material studied comes from parts of northern Spanish Sahara, north-western Mauritania, and southern Morocco (see Map, text-fig. 1). This area is occupied by the Palaeozoic Tindouf Basin, the Middle Devonian of which has been described



TEXT-FIG. 1. The geography and Devonian outcrop of the Tindouf Basin and adjacent regions.



TEXT-FIG. 2. Fossil localities and Middle Devonian outcrop on the southern flank of the Tindouf Basin.

by Arden and Rehrig (1964) and Sougy (1964). Within this succession lies the *Werneroceras* Limestone, the only known source of the new subspecies. This limestone is a constant marker horizon throughout the Tindouf Basin and contains the goniatites *Werneroceras crispiforme* (Kayser) and *Anarcestes* (*Anarcestes*) *lateseptatus* (Beyrich), the presence of which suggests a late Eifelian to earliest Givetian age. The *Werneroceras* Limestone is subject to lateral facies changes, and varies from a blue-grey limestone to a calcareous marl, the latter called by Sougy (1964) the Marno-calcaires à *Phacops fecundus*. The main fossil locations lie around Aïn Terguet (see Map, text-fig. 2), but to the south a form identical with *P. rana tindoufensis* has been reported from the same horizon at Aguelt Oudiate et Khyam (Sougy 1964). A further specimen was collected by Le Maître from the area of Zagora in southern Morocco. No Devonian exists in this latter place but, from the evidence of the southern area, the specimen is likely to belong to the same horizon as the others, and is presumably from the nearest Devonian—that of Tafilalet.

These trilobite horizons of North-West Africa can be correlated with those of North America containing *P. r. milleri* and *P. r. crassituberculata* using the work of House (1962). House has suggested (1962, p. 254) that *Werneroceras crispiforme* (≡ *Cabrieroceras crispiforme*) of Europe and North Africa is very closely comparable with the American *Werneroceras plebeiforme* (Hall), both in morphology and restricted stratigraphical occurrence. The latter occurs in the *Werneroceras* Bed at the top of the Union Springs Member of the lowest part of the Marcellus Formation. Therefore on this reasoning *P. rana africanus* and *P. r. tindoufensis* can be correlated stratigraphically with *P. r. milleri* and *P. r. crassituberculata* which first appear in the lower parts of the Marcellus Formation in the states of New York and Ohio. Migration of phacopid trilobites from the Old World to the New World was first hinted at by Hall and Clarke (1888, p. 24) who noted that *P. rana* appears to be more similar to European species of *Phacops* than to any other known North American species. Their conclusion has been substantiated by Eldredge (1972) and by the authors further on in this paper. Moreover, Eldredge (1972) has concluded that *P. rana* was derived from 'European' ancestors and was a migrant into the Hamilton (Middle Devonian) fauna of North America. The demonstration of the presence of *P. rana* in North-West Africa, while not sufficient in itself to indicate directions of migration, nevertheless tends to support this view. Further evidence that such a route was open is provided by *Greenops* (*Greenops*) *boothi* (Green 1837), the only member of the Asteropyginae known to occur in North America. The Asteropyginae are well represented throughout the Devonian of Europe, and in the Lower Eifelian of the Saoura Basin (Le Maître 1952), the Pragian of Central Morocco (Alberti 1969), and the Lower and Middle Devonian of the Tindouf Basin (Sougy 1964). With a single doubtful exception the earliest occurrence of *Greenops* is in the Marcellus Formation of New York and adjacent states, coincident with the earliest occurrence of the Hamilton fauna. There can be no question that *Greenops* is an immigrant trilobite. *Phacops rana crassituberculata* first appears at about the same time, and it is quite likely that the migration histories of the two species were similar.

That a migration route existed between North-West Africa and North America is suggested by Sutton's (1968) work on continental drifting and the proto-Atlantic, in which he suggests a close Devonian fit between Africa and South, Central, and Southern North America. Sougy (1962) has also linked the North-West African Palaeozoic Fold Belt with that of the Appalachians. It also seems likely that a shelf environment persisted right across the proto-Atlantic, since vagrant benthos such as phacopids (Clarkson 1966, p. 82) could only have migrated under such conditions. Furthermore, the absence of phacopids in the known Arctic Devonian faunas of North America (Ormiston 1967) taken together with the above arguments strongly supports a direct faunal connection along the route North-West Africa–southern North America–east-central North America.

SYSTEMATIC PALAEONTOLOGY

Family PHACOPIDAE Hawle and Corda, 1847
(nom. correct. Salter 1864 (pro Phacopides Hawle and Corda, 1847))
Subfamily PHACOPINAE Hawle and Corda, 1847
(nom. transl. Reed 1905 (ex Phacopidae Hawle and Corda, 1847))
Genus PHACOPS Emmrich, 1839
Phacops rana (Green, 1832)

Emended diagnosis (Eldredge 1972). Eyes large, bearing from 15 to 18 dorso-ventral files of lenses in normal adults. Trace of facial suture over ocular platform shallow. Genal angles gently rounded and near ventral cephalic margin. Glabella furrow 1p deeply incised, glabellar furrows 2p and 3p weakly developed or absent. Cephalon covered by low, rounded tubercles becoming transversely elongate at the anterior margin of the glabella, on the genae, and on the occipital lobe. Tubercles largest on central region of composite glabellar lobe and glabellar lobe 1p. Axis of thorax covered with transversely elongate tubercles. Tuberculation on pleura variably developed.

Pygidium with from 7 to 11 axial rings and 6 or 7 pleura. Tubercles moderately elongate transversely on axis; tubercles cover pleura, becoming obsolescent on pygidial margin. Interpleural furrows generally obsolescent, anteriormost interpleural furrow occasionally present as shallow groove set off by parallel rows of tubercles. Pleural furrows rather shallow, pleura only moderately arched.

Phacops rana africanus subspecies nov.

Plate 47, figs. 8–9; Plate 48, figs. 1–4

1939 *Phacops latiforns* Bronn; Le Maître, p. 203.
1964 *Phacops schlotheimi* Bronn; Arden and Rehrig, p. 1522.

Deriv. nom. Africanus, of Africa, referring to the fact that this is the first subspecies of *Phacops rana* to be recognized in Africa.

Localities. Tifariti area, Spanish Sahara; Gor Loutad, Spanish Sahara; Zagora, Tafilalet, Morocco.

Horizon. Werneroceras Limestone, Upper Eifelian–Lower Givetian boundary, Middle Devonian.

Material. 10 specimens, sample numbers USNM 174227 and USNM 174072, 'Aïn Terguet formation' (American field usage) equivalent to *Werneroceras* Limestone, and Marno-calcaires à *Phacops fecundus* of Sougy (1964), Gor Loutad, Spanish Sahara; 3 specimens SUI, locality unknown, Spanish Sahara; 7 specimens, sample numbers In 56876–56878, 57166–57167 (Rod collection) and It 5821–5822 (Illing collection) BMNH, Tifariti area, Spanish Sahara; 3 specimens AMNH numbers 29130–29132 from the lowest Givetian (Unit 4b of Arden and Rehrig 1964) of the Gor Loutad region, Spanish Sahara (location at 10° 30′ W., 26° 45′ N.); 1 specimen ULL, Zagora, Tafilalet, Morocco. (For locations see Map, text-fig. 2.)

Holotype. USNM number 174072, *Werneroceras* Limestone, Gor Loutad, Spanish Sahara.

Diagnosis. Eyes small and with large eye socle. Intercalating ring very weakly developed. Glabellar tubercles very large, not elongated anteriorly. Ornament of palpebral lobe and fixigenal eye stem sparse and large. Occipital ring ornament very sparse or missing. Genal ornament sparse.

Description. Large trilobites with cephalic lengths (sag.) ranging from 14·8 to 32·4 mm; cephalic outline roughly semicircular, posterior margin curved only slightly anteriorly, genal angles smoothly rounded and parabolic. In side view the glabella is inflated and rises vertically, or with a slight anterior bulge, in a smooth arc to a nearly flat summit level. The slightly arched top of the glabella then drops gently down to the intercalating ring, which is low and unobtrusive. The wide occipital ring projects strongly and has a vertical posterior face. The axial furrows diverge at angles varying from 55° to 68° with an average of 63°. The broad glabella is terminated at the rear by a wide intercalating furrow, and its anterior margin is a smooth curve. The 2p and 3p glabellar furrows are present, the latter being visible as a pair of short furrows on the natural cast. The glabellar ornament consists of numerous large hemispherical or flat-topped tubercles which are fairly widely separated at the posterior, but which become smaller and more closely packed anteriorly to form tesselations, on the anterior face of the glabella. The average diameter of the posterior tubercles is 1·5 mm for the range of cephalic lengths given. The intercalating ring is always low and narrow, the axial lobe is ornamented with a single large, laterally elongated tubercle, or occasionally two small tubercles. The occipital ring is wide, prominent, and is either smooth or has low randomly distributed central tuberculations. The tubercles when present are transversely elongated.

The eyes are large and set high on the genae almost reaching the level of the top of the glabella. The eye socles are wide and steeply inclined. The visual surfaces are nearly vertical with always 18 dorso-ventral files of eye lenses, in these samples the eyes contain 70–80 lenses (Table 1) set flush with strong hexagonal rims of sclera.

TABLE 1. Measurements and eye data for *P. rana africanus* subsp. nov. *Werneroceras* Limestone, Givetian, Spanish Sahara.

CL—total cephalic length; WBVS—width between visual surfaces; N LENS—total number of lenses on visual surface; # DV—number of dorso-ventral files. Measurements in centimetres.

CL	WBVS	EYE FORMULA	EYE	N LENS	# DV
1.73	—	345 555 555 454 433 332	L	73	18
2.20	2.75	445 555 555 454 434 332	L	75	18
2.30	3.00	345 455 555 454 433 232	L	71	18
2.37	3.17	455 555 555 454 434 332	R	76	18
2.40	3.10	455 555 555 554 433 332	L	76	18
2.47	3.52	455 555 555 554 434 332	L	77	18
2.91	4.46	455 565 655 554 444 332	L	80	18
3.24	4.71	455 565 655 554 444 332	L	80	18
3.50	4.50	455 555 655 554 444 332	L	79	18
3.90	4.90	455 555 555 554 444 332	L	78	18

There is a maximum of 6 lenses per dorso-ventral file. The palpebral lobes are crescent-shaped with large tubercles, and the fixigenal eye stems are rounded and bear a cluster of a few large tubercles on their anterior distal extremities. They are extended into small, low, rear-eye ridges ending against the facial sutures.

The palpebral furrows are strongly accentuated. The genae are flexed strongly downwards and are usually smooth or possess at the most a single posterior row of tubercles. The posterior marginal ridge is prolonged into a wide, flat, lateral area slightly elevated above the fixigena. The vincular furrow possesses 7 cusp-like projections on its inner wall at a point below the eye. The hypostome is unknown. The thorax carries little ornament, the axial segments having very low, randomly distributed, central tuberculation together with a posterior row of tubercles. The pleurae are smooth. There is a constriction (ex-sag.) near the distal ends of the axial segments forming incipient nodes. The pygidium has 9–11 axial rings and 6–7 pleurae. It has no ornament.

Measurement and eye data: see Table 1.

Discussion. Phacops rana africanus is discussed below in conjunction with *Phacops rana tindoufensis.*

Phacops rana tindoufensis subspecies nov.

Plate 47, figs. 1–3

1964 *Phacops* (*Phacops*) *fecundus degener* (Barrande); Sougy, p. 447, pl. 41, figs. 5, 5*a*.

Deriv. nom. Tindoufensis, of the Tindouf Basin.

Localities. USNM locality H-23, 4 miles south of the junction of Oued Ratmia and Oued Aïn Terguet, about 1 mile west of Oued Ratmia, south-west Tindouf Basin, Spanish Sahara. Also region between Smara and Tifariti, 11° 15′ W., 26° 39′ N.

Horizon. Shales interbedded with *Werneroceras* Limestone, Upper Eifelian–Lower Givetian boundary, Middle Devonian.

Material. 5 specimens, USNM number 174228, and 1 specimen USNM number 174073, from the shales of the *Werneroceras* Limestone, USNM locality H-23. 6 specimens, AMNH numbers 29133–29138, from the Smara–Tifariti region, from the same limestone as *Phacops rana africanus* but at a point where it is less silty, Unit 4b of Arden and Rehrig (1964).

Holotype. USNM number 174073, from the *Werneroceras* Limestone at USNM locality H-23.

Diagnosis. Eyes with most lenses protruding beyond interlensar sclera, except for top 2 to 3 lenses of each dorso-ventral file which are flush with sclera. Intercalating ring well developed but narrow. Glabellar tubercles elongated transversely close to anterior glabellar margin in some cases, otherwise merely flattened. Whole of dorsal exoskeleton richly ornamented.

Description. Small trilobites with cephalic lengths (sag.) ranging from 9·0 to 17·0 mm; cephalic outline slightly wider than semicircular, posterior margin curved only slightly anteriorly, genal angles smoothly rounded but never parabolic. In side view the glabella is scarcely at all inflated and rises vertically, or slightly less than vertically, to a flat summit level. This flat surface then drops gently down to a pronounced intercalating ring. There is a wide occipital ring. The axial furrows diverge at angles approaching 65°. On the glabella 2p and 3p glabellar furrows are visible, but only faintly impressed. The glabellar ornament consists of numerous small to medium-sized rounded to conical tubercles, evenly distributed posteriorly, becoming smaller and more closely packed anteriorly, but never forming tesselations. In some cases those tubercles closest to the anterior glabellar margin become flattened and elongated transversely (Sougy 1964, pl. 41, fig. 5*a*). The average diameter of the posterior tubercles is 0·7 mm. The intercalating ring is pronounced but narrow, the axial lobe being ornamented with one or two equidimensional tubercles. The occipital ring is wide and prominent and has numerous randomly distributed tubercles, all of which are flattened and elongated transversely. The eyes are rather short compared with the length of the cephalon. The eye socles are narrow and insignificant. The visual surfaces are tall and slightly less than vertical with 18 dorso-ventral files, a maximum of 9 lenses per dorso-ventral file, and an average of 109 lenses per eye (Table 2). The lenses are closely spaced and protrude beyond the interlensar sclera

TABLE 2. Measurements and eye data for *P. rana tindoufensis* subsp. nov. *Werneroceras* Limestone, Givetian, Spanish Sahara. Abbreviations as in Table 1 (above).

CL	WBVS	EYE FORMULA	EYE	N LENS	# DV
1.70	2.00	567 787 877 776 655 432	R	107	18
0.90	1.10	566 676 767 665 655 332	L	97	18
1.35	1.65	567 777 777 676 655 442	L	105	18
1.00	1.20	678 898 888 877 767 543	R	124	18
1.20	1.40	568 787 878 776 655 442	R	110	18

near the bottom of the dorso-ventral files, and are more widely spaced and flush with the sclera near the tops of the dorso-ventral files. The palpebral lobes are crescent-shaped with small tubercles, and the fixigenal eye stems are flattened and bear numerous, evenly distributed, small tubercles. They are extended into small, low rear-eye ridges ending against the facial sutures. The palpebral furrows are moderately accentuated. The genae are not strongly flexed downwards and are abundantly ornamented with a single row of posterior tubercles, and small, randomly distributed, tubercles on the rear halves of the genae, these tubercles fading out anteriorly. The posterior marginal ridge is weak and does not persist laterally beyond the rear of the eye. The hypostome is unknown.

Flattened tubercles, elongated transversely, cover the axial rings of the thorax and pygidium. The posterior ramus of the pleura in the thorax and pygidium is covered densely with low, rounded tubercles. There is a constriction (ex-sag.) near the distal ends of the axial rings of the thorax forming incipient nodes. The pygidium has 9 or 10 axial rings and a terminal piece, and 7 pleurae. 1 pair of interpleural furrows are present.

Measurements and eye data: see Table 2.

Comparisons. The pair *Phacops rana tindoufensis* and *P. r. africanus* are close to the American pair *P. r. milleri* and *P. r. crassituberculata*, these 4 also forming a small complex distinct from all other subspecies of *P. rana*. Moreover, within this com-

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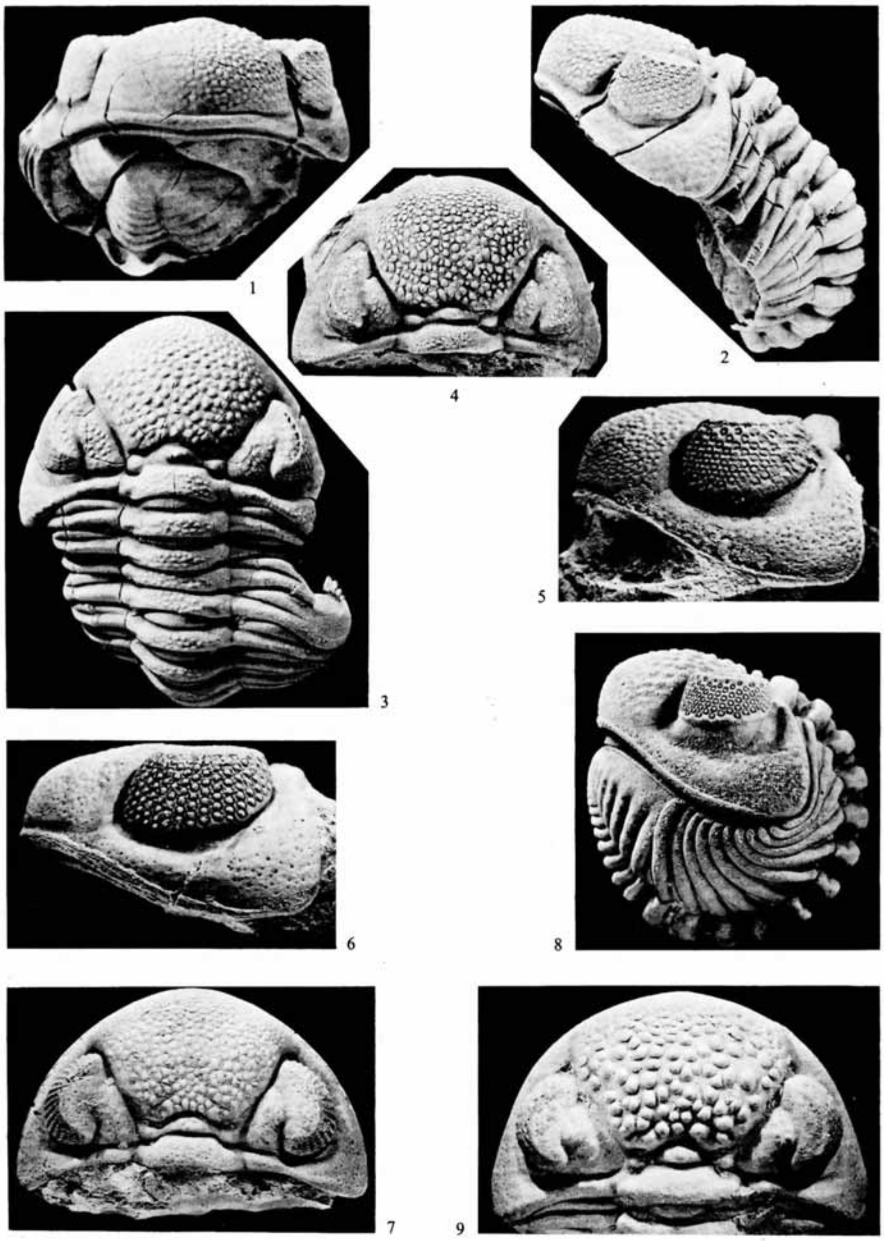
EXPLANATION OF PLATE 47

Figs. 1–3. *Phacops rana tindoufensis* subsp. nov. Holotype, USNM 174073. All ×2. Givetian, USNM loc. H-23, 11° 15′ W., 26° 39′ N., Spanish Sahara.

Figs. 4–5. *Phacops rana crassituberculata* Stumm, AMNH 28898. 4, ×2. 5, ×3. Lower Cazenovian, Ohio, U.S.A.

Figs. 6–7. *Phacops rana milleri* Stewart, AMNH 28896. 6, ×2. 7, ×3. Lower Cazenovian, Ohio, U.S.A.

Figs. 8–9. *Phacops rana africanus* subsp. nov. Holotype, USNM 174072. 8, ×1·5. 9, ×1·5. Givetian, Gor Loutad, Spanish Sahara.



BURTON and ELDREDGE, *Phacops rana* ssp.

plex *P. r. tindoufensis* compares closely with *P. r. milleri*, and *P. r. africanus* with *P. r. crassituberculata*, although less closely. The reasons for this latter pairing will be made clear by the comparison between *P. r. tindoufensis* and *P. r. africanus*. This brings out critical differences which are also valid for differentiating between the pairs *tindoufensis–milleri* and *africanus–crassituberculata*.

The critical differences between *P. r. tindoufensis* and *P. r. africanus* can be divided into those of major structural features and those of ornament. In *P. r. tindoufensis* (Pl. 47, figs. 1–3) the genal angles are rounded but never parabolic, the intercalating ring is pronounced, the eyes large with a maximum of 9 lenses per dorso-ventral file and with lenses projecting beyond the interlensar sclera. The fixigenal eye stems are flattened. The ornament is generally rich, with glabellar tubercles being conical to rounded and of small to medium size, those along the anterior margin being transversely elongated. The palpebral lobes, fixigenal eye stems, occipital ring, and the genae bear numerous low tubercles. The thorax is also well ornamented. The corresponding features in *P. r. africanus* (Pl. 47, figs. 8, 9; Pl. 48, figs. 1–4) show clear differences, the genal angles being always parabolic, the intercalating ring low, the eyes smaller with a maximum of 6 lenses per dorso-ventral file, and the lenses set flush with the sclera. The fixigenal eye stems are rounded. The ornament is sparse with large hemispherical or flattened glabellar tubercles which are never transversely elongated along the anterior glabellar margin. The palpebral lobes and fixigenal eye stems have small numbers of large tubercles, and the occipital ring may be devoid of tubercles or have very few large ones. The genae never bear more than one row of tubercles, these being always on their posterior margins. This latter pattern is followed in the thoracic pleurae.

P. r. tindoufensis and *P. r. milleri* (Pl. 47, figs. 1–3, 6–7) show remarkably few differences. The eye of the latter is longer compared with the length of the cephalon than that of the former; and although the eye details are almost identical, only the topmost lenses of each dorso-ventral file are flush with the interlensar sclera in *P. r. milleri*, whereas in *P. r. tindoufensis* the upper two or three lenses in each file are flush with the sclera. The intercalating ring of *P. r. milleri* is marginally more pronounced than that of *P. r. tindoufensis*, and the distal portions of the thoracic axial rings of the latter (Pl. 47, fig. 2) are always constricted into incipient nodes. This node formation is never seen in *P. r. milleri*. The only other differences are those of ornamentation, in *P. r. milleri* the flattened, transversely elongated tubercles occur well up the anterior slope of the anterior glabellar lobe, whereas those of *P. r. tindoufensis* are restricted to the most anterior part of the lobe or are not present at all (Pl. 47, fig. 1). Also in the American subspecies the glabellar tubercles are more closely packed and sometimes, viewed from above, are more polygonal than rounded, whereas those of the African subspecies are slightly less crowded and always rounded. The amount of ornament is noticeably less, although of the same type and in the same places, on the genae, thorax, and pygidium of *P. r. milleri*, than that on *P. r. tindoufensis*.

The comparison *P. r. africanus–P. r. crassituberculata* yields differences of somewhat greater magnitude, but again more of degree than kind. The most noticeable difference lies in the size of the eye. That of *P. r. africanus* is relatively small and lies high on the gena, whereas that of *P. r. crassituberculata* is larger and occupies more of the gena (Pl. 47, figs. 5, 8). Correspondingly the former's eye socle is larger and the latter's small. In all other features the eyes are identical. Differences in size and distribution of ornament are marked, the American subspecies being the more richly ornamented. Elongated tubercles are common on the anterior portion of the anterior glabellar lobe of *P. r. crassituberculata*, but are not present on *P. r. africanus*. Furthermore, although the glabellar tubercles are arranged in much the same fashion and have the same shapes in the two subspecies, those of *P. r. crassituberculata* are considerably smaller than those of *P. r. africanus*. This size difference is again seen in the ornament of the palpebral lobe and fixigenal eye stem, that of the American subspecies being much smaller than that of the African subspecies. In contrast the occipital ring of *P. r. africanus* has either no ornament or a few low transversely elongated tubercles, whereas that of *P. r. crassituberculata* always has many, small, transversely elongated tubercles. Genal ornament is much the same size in both subspecies but is confined to the rear of the genae in *P. r. africanus*, occupying over half the genae in *P. r. crassituberculata*.

The only other differences are seen in the thorax and pygidium. The distal ends of the thoracic axial rings of the African subspecies have a slight constriction which is unknown in the American subspecies, and the pygidium of the African subspecies has 9–11 axial rings to a maximum of 9 in the American subspecies.

Although at first sight there might appear to be a wide gap between the two subspecies, this is illusory when details are considered. Eye details which in general indicate fundamental differences are identical, except for the actual size of the eye. The ornament of course is of discriminatory value but at the subspecific level. Other basic characters even of some subspecific value are identical. These characters include (Pl. 47, figs. 4, 5, 8, 9; Pl. 48, figs. 1, 3, 4) intercalating ring form, cephalic outline and profile, genal angle shape, angle between axial furrows (average 63°), rear-eye ridges. Furthermore, the pairings *P. r. milleri–P. r. tindoufensis* and *P. r. crassituberculata–P. r. africanus* are the only admissible ones between American and African subspecies, since the two pairs have different morphological characteristics, as stated above. The *milleri–tindoufensis* pair share the strongly accentuated intercalating ring, flattened fixigenal eye stems, distinct eye features, genal angle shape, and ornamental features which cannot be duplicated within the pair *crassituberculata–africanus*.

Comparisons with other North African species: the specimen illustrated by Sougy (1964, p. 447, pl. 41, fig. 5) and identified by him as *P. (Phacops) fecundus degener* belongs to *P. rana tindoufensis*. Further, *P. r. tindoufensis* bears a resemblance to *P. menchikoffi* Le Maître from the Lower Eifelian of the Saoura Basin. However, *P. menchikoffi* possesses fewer lenses per dorso-ventral file, and appears to have small, sparsely scattered tubercles on the anterior glabellar lobe.

P. speculator from the Eifelian of western Morocco has been compared by Alberti (1970) with *P. rana milleri*. However, although it is clearly allied to *P. rana*, it lacks the dense development of tubercles of the *tindoufensis–milleri* pair, and is closer to *P. menchikoffi*.

It is apparent that *P. rana* (s.l.) is widely represented in North-West Africa, and it appears to one of us (C. J. B.) that there may be links between the North-West African representatives of this species and the *P. schlotheimi* (s.l.) group of the

Old World. *P. schlotheimi* (s.s.) (Burton 1969 for morphological details) bears only a general resemblance to either *P. rana africanus* or *P. r. tindoufensis* and cannot be considered directly ancestral. However, members of the *P. schlotheimi* (s.l.) group are known to exist in the French Pyrenees (Cavet and Pillet 1958, p. 21), Morocco (Richter 1943), and in the Saoura Basin of Algeria (Le Maître 1952, p. 156).

The Algerian form (Pl. 48, figs. 5–6) is a new subspecies of *P. schlotheimi* of Lower Eifelian age and appears to have characters intermediate between *P. schlotheimi* s.s. and *P. rana tindoufensis*. However, the authors do not at this time intend to press this similarity any further, being content to maintain that there are sufficient North-West African representatives of the group of *P. schlotheimi* (s.l.) to have provided an ancestral complex to the *P. rana* group and that few other groups are thus situated.

Discussion. The comparisons have shown that the African subspecies *P. rana tindoufensis* and *P. r. africanus* are, respectively, close to the North American subspecies *P. r. milleri* and *P. r. crassituberculata* recently redescribed by Eldredge (1972). The differences separating the subspecies in each continent parallel one another to a remarkable degree, and the four subspecies appear to form a complex distinct from all the other subspecies of *P. rana*. The nature of this complex is not yet fully understood. Eldredge (1972) has shown that *P. r. milleri* and *P. r. crassituberculata* do not generally occur together in the same fauna. Their geographical distribution does overlap, especially in northern Ohio and southern Michigan where both are known from the Silica Shale fauna. However, they rarely occur in the same unit. *P. r. crassituberculata* shows a marked 'preference' for relatively pure limestone, while *P. r. milleri* is usually found in calcareous shales. A complicating factor is that the two eye variants are occasionally found in association, and that all small (meraspid(?) and early holaspid) cephala from the Silica shale show *milleri*-type bulging lenses, indicating that the early ontogeny of the eye in both *P. r. milleri* and *P. r. crassituberculata* was probably the same. It is tentatively concluded that the *milleri* and *crassituberculata* eye variants probably represent a stable situation in population genetics, where local populations are adapted to harder substrates and presumably cleaner water (*P. r. crassituberculata*) or softer, muddier substrates, hence more turbid water (*P. r. milleri*). Alternatively, the ontogeny of the eye might have been capable of responding to local conditions, i.e. possesses a broad 'norm of reaction'. However, the precise nature of this relationship cannot be explained on the data available, but in view of the relative ease of differentiation of the variants Eldredge concludes that the best course is to continue to treat them as subspecies. In any case, this mode of interpopulation variation is peculiar to the above two subspecies of *P. rana* in North America.

A similar situation appears to exist for *P. r. africanus* and *P. r. tindoufensis*, both

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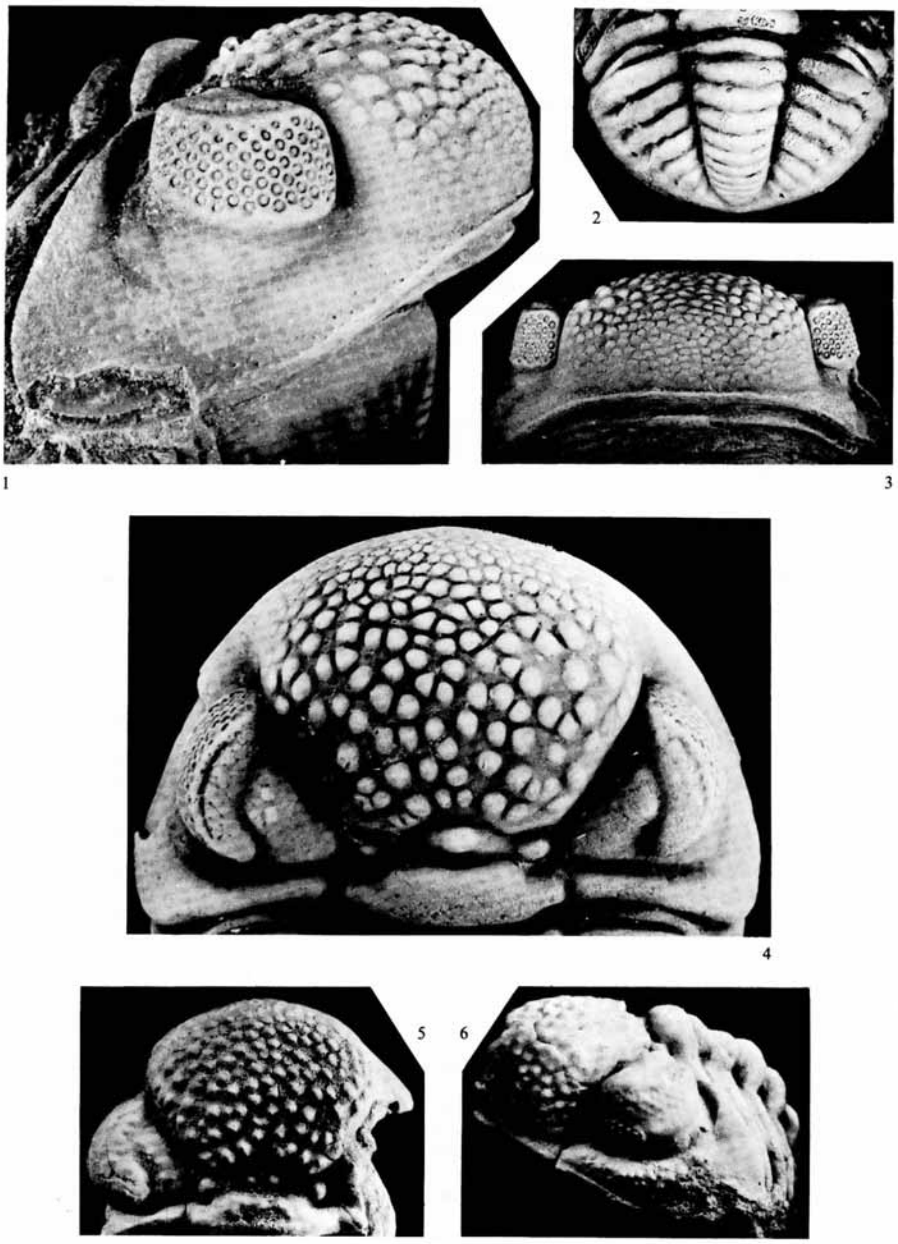
EXPLANATION OF PLATE 48

Figs. 1–4. *Phacops rana africanus* subsp. nov. 1, In 57166, ×2. 2, In 56877, ×1. 3, In 57166, ×1. 4, In 57166, ×2. Givetian, Tifariti area, Spanish Sahara.

Figs. 5–6. *Phacops schlotheimi* ssp., ULL 256 d 49, a–b. 5, ULL 256 d 49 b, ×3·4. 6, ULL 256 d 49 a, ×3·2. Eifelian, Erg Djemel, Algeria.

PLATE 48



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forms being found at the same horizon, the *Werneroceras* limestone. This varies in lithology from a more or less pure limestone to a calcareous marl, and the two subspecies are found in different facies. *P. r. africanus* is found in the relatively pure limestones, silty limestones, and coarsely sandy calcareous beds, whereas *P. r. tindoufensis* is found in shales and marly limestones. There are obvious parallels with the situation cited above by Eldredge, although the two subspecies are not quite as close as the American ones and locality detail is by no means as precise, which limits the rigour of the comparison. However, it is beyond coincidence that a similar adaptional pairing should be found in African subspecies of *P. rana* which are individually closely similar to one or other of the American pair. This therefore suggests that the African subspecies are related in the same fashion as the American subspecies and that there was likely to have been communication between the two areas during the Middle Devonian.

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